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Spatial attention processing priorities modulate distributed spatial representations in the occipital visual cortex

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Abstract

Visual selective attention (VSA) is a cognitive function that biases the perceptual processing of visual inputs on the basis of their behavioral relevance. The brain correlates of VSA have mostly been studied in terms of biases of the spatial representations in the occipital cortex, or the functional responses of attention controlling networks in the frontoparietal cortex (FPAN). These two main research fields made use of disparate paradigms and led to contradictory findings, precluding their integration into a unified framework. An emerging theoretical account, the priority maps framework, attempts to reconcile these contradictory findings into a unified view. It posits that an attentional gating is observable within spatial maps in the brain, as a function of the behavioral relevance of items in the visual field and their spatial location, arising from computations both at the occipital and the FPAN levels. However, so far, this account has received poor experimental support. Across three fMRI studies, we tested how multiple spatially-distributed attentional signals bias the spatially-specific responses in the occipital cortex and explored the mechanisms governing these bias. In all studies, we used a visual display containing four items, including one target, placed each in one of the four screen quadrants. Across experiments, we manipulated the configuration of the visual display by incorporating salience (all experiments), goal-directed endogenous cues (Experiment 1), statistical regularities (Experiment 2) and reward (Experiment 3). The main analyses sought to characterize how the different gating signals affect the activity of distributed spatial representations in the visual cortex and whether/how they interact within these representations. For this we constructed a 2D index (spatial bias vector) that, using the activity of multiple quadrant-specific occipital regions, provides us with a measure of the strength and direction of the overall attentional gating. We carried out these analyses in three separate occipital Brodmann areas (BA17, BA18, BA19) in order to capture the contribution of the attentional signals throughout the visual hierarchy. We explored the mechanisms governing the observed spatially-specific patterns of activity in the occipital cortex using interregional connectivity analyses between the parietal and the occipital cortex and performing whole-brain analyses. We showed that, across the three experiments, all attentional signals impacted the response patterns of spatially-specific activity in the occipital cortex. However, these signals had specific signatures that could be explained in terms of top-down signaling involving the FPAN (Experiment 1), but also local interactions within the occipital cortex (all experiments). This work sheds new light on the specification of the mechanisms and constraints that govern the selection of relevant information in conditions entailing a multitude of competing signals, emphasizing for the first time the key contribution of spatial representations in the occipital visual cortex.

Résumé

L'attention sélective visuelle (ASV) est une fonction cognitive qui biaise le traitement perceptuel d'entrées visuelles sur la base de leur intérêt comportemental. Les bases cérébrales de l'ASV ont principalement été étudiées en termes de biais des représentations spatiales dans le cortex occipital, ou de réponses au niveau des réseaux frontopariétaux du contrôle attentionnel (RFPCA). Ces deux champs de recherche principaux ont utilisé des protocoles disparates et ont mené à des résultats contradictoires, ce qui a entravé leur intégration dans un cadre théorique unifié. Un cadre théorique émergent, celui des cartes de priorités attentionnelles, tente de palier ces problèmes. Ce cadre théorique postule que l'intérêt comportemental d'items présents dans le champs visuel augmente l'activité des représentations spatiales de ces items au sein de cartes spatiales cérébrales, ceci étant sous-tendu par des computations au niveau occipital et du RFPCA. Toutefois, ce cadre théorique manque de support expérimental. A travers trois études en IRMf, nous avons testé comment différents signaux attentionnels biaisent les réponses spatialement spécifiques dans le cortex occipital. Dans chaque étude, nous avons utilisé des affichages visuels comprenant quatre items, dont un item cible, chacun étant disposé dans un des quatre quadrants de l'écran. Nous avons manipulé la configuration de ces affichages en incorporant de la saillance (toutes les expériences), de l'attention dite endogène (Expérience 1), des régularités statistiques (Expérience 2) et de la récompense (Expérience 3). Les analyses principales visaient à caractériser comment ces différents signaux attentionnels affectent l'activité des représentations spatiales dans le cortex occipital. Pour cela, nous avons calculé un index 2D (vecteurs spatiaux de biais attentionnel) sur la base de l'activité des représentations occipitales de chaque quadrant de l'écran qui permet de mesurer la force et la direction du biais attentionnel global dans chaque condition expérimentale. Ces analyses ont été conduites dans trois aires de Brodmann différentes (BA17, BA18, BA19) et ont été couplées à des analyses à l'échelle du cerveau entier et de connectivité inter-régionale permettant d'investiguer les sous-tendements cérébraux de la mise en place des biais attentionnels spatiaux dans le cortex occipital. A travers ces trois expériences, nous avons montré que tous les signaux attentionnels testés affectaient les patrons de réponses spatialement distribuées dans le cortex occipital. Toutefois, les mécanismes sous-tendant cette intégration au niveau occipital étaient propres à chaque type de signal, notamment avec un contrôle descendant ("top-down") impliquant le cortex pariétal dorsal (Expérience 1), mais aussi des computations intra-occipitales (toutes les expériences). Ce travail précise des mécanismes et contraintes qui sous-tendent la sélection d'informations pertinentes dans des conditions impliquant la présence de multiples signaux attentionnels en compétition dans le champ visuel, soulignant pour la première fois la contribution clé des représentations spatiales au niveau occipital.

Résumé substantiel

L'attention sélective visuelle (ASV) est une fonction cognitive qui biaise le traitement perceptuel d'entrées visuelles sur la base de leur intérêt comportemental. Les bases cérébrales de l'ASV ont principalement été étudiées en termes de biais des représentations spatiales dans le cortex occipital, ou de réponses au niveau des réseaux frontopariétaux du contrôle attentionnel (RFPCA). Ces deux champs de recherche principaux ont utilisé des protocoles disparates et ont mené à des résultats contradictoires, ce qui a entravé leur intégration dans un cadre théorique unifié. Un cadre théorique émergent, celui des cartes de priorités attentionnelles, tente de palier ces problèmes. Ce cadre théorique postule que l'intérêt comportemental d'items présents dans le champs visuel augmente l'activité des représentations spatiales de ces items au sein de cartes spatiales cérébrales, ceci étant sous-tendu par des computations au niveau occipital et du RFPCA. Toutefois, ce cadre théorique manque de support expérimental. A travers trois études en IRMf, nous avons testé comment différents signaux attentionnels biaisent les réponses spatialement spécifiques dans le cortex occipital.

Dans chaque étude, nous avons utilisé des affichages visuels comprenant quatre items, dont un item cible, chacun étant disposé dans un des quatre quadrants de l'écran. Nous avons manipulé la configuration de ces affichages en incorporant de la saillance (toutes les expériences), de l'attention dite endogène (Expérience 1), des régularités statistiques (Expérience 2) et de la récompense (Expérience 3). Les analyses principales visaient à caractériser comment ces différents signaux attentionnels affectent l'activité des représentations spatiales dans le cortex occipital. Pour cela, nous avons calculé un index 2D (vecteurs spatiaux de biais attentionnel) sur la base de l'activité des représentations occipitales de chaque quadrant de l'écran qui permet de mesurer la force et la direction du biais attentionnel global dans chaque condition expérimentale. Ces analyses ont été conduites dans trois aires de Brodmann différentes (BA17, BA18, BA19) et ont été couplées et des analyses à l'échelle du cerveau entier et de connectivité inter-régionale permettant d'investiguer les sous-tendements cérébraux de la mise en place des biais attentionnels spatiaux dans le cortex occipital.

Dans la première expérience, nous avons manipulé la pertinence comportementale relative au but, matérialisé par un indigage spatial qui indiquait aux participant.e.s, avec une prédictivité de 100%, dans quel quadrant de l'écran l'item cible allait apparaître. Conjointement, nous avons manipulé la saillance des items présentés à l'écran, matérialisée par trois conditions expérimentales distinctes : soit tous les items étaient de la même couleur (affichage homogène, AH), soit l'item cible avait une couleur différente des trois items distracteurs (affichage cible saillante, ACS), soit un distracteur avait une

couleur différente des deux autres distracteurs et de l'item cible (affichage distracteur saillant, ADS). Les résultats montraient que les vecteurs spatiaux étaient fortement biaisés vers la représentation occipitale du quadrant comprenant l'item cible. Ce biais était renforcé en condition ACS (dans BA18 et BA19) et réduit en condition ADS (BA17, BA18 et BA19). Ces résultats montrent que la pertinence comportementale relative au but et la saillance sont représentés conjointement dans le cortex occipital. A l'échelle du cerveau entier, aucune modulation significative d'activité n'a été détectée entre les trois conditions de saillance. Néanmoins, des analyses de connectivité effective entre le cortex pariétal postérieur (CPP, un noeud important du RFPCA) et le cortex occipital, ainsi qu'entre les représentations occipitales des quatre quadrants, ont révélé que les conditions de saillance modulaient la connectivité entre le CPP et le cortex occipital, mais aussi en intra-occipital. Ces résultats montrent que le traitement commun de la pertinence comportementale relative au but et de la saillance implique des computations pariétales-occipitales mais également occipitales-occipitales.

Dans la seconde expérience, nous avons manipulé les régularités statistiques dans l'espace (déséquilibre de la probabilité pour l'item cible d'être présenté dans chaque quadrant: un quadrant dans lequel la présentation de la cible était hautement probable, cible hautement probable : CHP ; et trois quadrants dans lesquels elle était faiblement probable, Cible faiblement probable : CFP) et la saillance de la même manière que pour la première expérience. Nous avons constaté que les vecteurs spatiaux étaient plus fortement biaisés vers la représentation spatiale occipitale de l'item cible en conditions AH et ACS qu'en condition ADS, comme lors de la première expérience. Par contre, le biais n'était pas significativement plus accentué en condition ACS qu'en condition AH. Les analyses ont révélé un effet des régularités statistiques uniquement dans BA17, où le biais des vecteurs spatiaux vers la représentation de la cible était plus faible en condition CHP qu'en condition CFP. Cet effet n'a pas été observé dans BA18 et BA19. Les analyses à l'échelle du cerveau entier ont montré que la saillance et les régularités statistiques modulaient les réponses dans le CPP. Des analyses de connectivité fonctionnelle entre le CPP et les trois aires occipitales testées ont montré que les régularités statistiques affectaient la connectivité fonctionnelle entre le CPP et BA18/19 mais pas entre le CPP et BA17. Ceci suggère que la modulation du biais des vecteurs spatiaux en fonction des régularités statistiques observé dans BA17 ne requierait pas de contrôle descendant ("top-down") en provenance du RFPCA.

Dans la troisième expérience, nous avons manipulé la récompense dans l'espace (un quadrant pour lequel une récompense importante était délivrée lorsque la cible qui s'y trouvait était détectée, Quadrant Hautement Récompensé : QHR; et trois quadrants pour lesquels une faible récompense était délivrée: Quadrant Faiblement Récompensé : QFR). Comme dans les deux expériences précédentes, nous avons observé que la

saillance affectait la magnitude des vecteurs spatiaux, mais uniquement en condition QFR. De plus, en condition QHR, la magnitude des vecteurs spatiaux était réduite en comparaison avec la condition QFR. Ces résultats concordent avec l'idée selon laquelle les signaux attentionnels relatifs à la récompense peuvent, dans certaines conditions, être "supprimés" de manière à ce que ces signaux n'interfèrent pas avec la tâche à accomplir. Les analyses à l'échelle du cerveau entier ont montré que la saillance, comme dans la seconde expérience, modulait les réponses dans des zones du RFPCA. A l'inverse, la récompense ne modulait pas les réponses dans ces zones. Ceci suggère que la suppression observée au niveau occipitale peut prendre place à long terme sans impliquer un contrôle descendant soutenu en provenance du RFPCA.

Ensemble, ces trois expériences nous ont permis de tester l'hypothèse selon laquelle le cortex occipital comprend des représentations spatiales des priorités attentionnelles. Dans le cadre de la théorie des cartes de priorités attentionnelles, nous avons évalué les modulations d'activité spatialement spécifique dans le cortex occipital par plusieurs signaux attentionnels (pertinence relative au but, saillance, régularités statistiques, récompense) présentés conjointement dans le champ visuel. Tous ces signaux ont affecté les réponses spatialement distribuées dans le cortex occipital. Néanmoins, ces effets étaient médiés par des mécanismes cérébraux spécifiques à chaque type de signal, incluant un contrôle descendant (Expérience 1), ou des computations intra-occipitales (toutes les expériences). Ce travail précise des mécanismes et contraintes qui sous-tendent la sélection d'informations pertinentes dans des conditions impliquant la présence de multiples signaux attentionnels en compétition dans le champ visuel, soulignant pour la première fois la contribution clé des représentations spatiales au niveau occipital.

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"Accept uncertainty. Be thoughtful, open and modest."
Ronald L. Wasserstein, Allen L. Schirm & Nicole A. Lazar
in *Moving to a World Beyond "p < 0.05"*

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Chapter 1

Introduction

Imagine a world just as the one we live in, but where suddenly there are no more odors, sounds, textures or tastes: only visual signals. In such an environment, organisms only equipped with receptors to odors, textures, tastes and/or sounds would no more be able to catch the visual preys, to run away from the visual predators or to breed with their visual mates. They would easily die and have difficulties to generate newborns. On the contrary, organisms equipped with visual receptors would more easily be able to catch the visual preys, to escape from the visual predators and to reproduce. This thought-experiment reflects how organisms only persist when and where they fit specific environmental conditions. In the real world, they have - among other things - to deal with food availability, predation, temperature, pressure or light constraints. This implies that organisms are able to behave in such a way that: 1) they do not die too easily (e.g. being able to get enough nutrients); and 2) they maximise their reproduction success. These two implications constitute the boundary conditions of life persistence: survival chances and reproduction chances.

A specific term gathers these boundary conditions: fitness. Fitness is defined as the capacity of an organism to survive and to reproduce in an effective manner, giving rise to fertile progenies. According to the fitness principle (e.g. see Thomas *et al.*, 2016), population pruning operates through time in such a way that individuals that are best adapted to the current environment will have good chances to generate (genetically) similar (next generation) individuals. Conversely, individuals that do not fit the current environment will have very few chances to generate new organisms. This process is called natural selection and constitutes the general evolutionary explanation of the introductory example: an organism facing a constraining event (e.g. necessity to find nutrients or to avoid a predator) has to be able to react not to die and to maximise its fitness. This evolutionary process in turn equips organisms with adequate physiological features over generations. What equipment do organisms need to fit the world? Of course, this depends on time and space: organisms living in the trees of the Amazon forest several thousand years ago or near the ocean floor nowadays would not need the same

physiological equipment to maximise their fitness. But there are constants. For example, as mentioned in the introductory example, the ability to sense the world seems to be a major prerequisite for life persistence. Indeed, this is what provides organisms with information about the external world (e.g. nutrients availability, presence of predators, temperature, etc). This ability to sense the world has been conceptualized under a host of terms, including "perception", "sensation", "observation", etc (Efron, 1969; Raftopoulos, 2001).

Conceptual distinctions between those terms concern the degree to which the "sensing" purely reflects the state of the environment: from a very pure, unbiased sampling of the external signals to a cognitively biased sensing apparatus. While the definition of the term "sensation" as being a very pure sensing of the world seems consensual (Efron, 1969), intense debates exist concerning the pure, cognitively unbiased nature of "perception" (Efron, 1969; Raftopoulos, 2001; Powers *et al.*, 2016). From the various attempts of defining what perception is and how it works (e.g. Efron, 1969; Raftopoulos, 2001; Powers *et al.*, 2016; Lupyan, 2017), one can broadly define perception as being the representation of information provided by the senses. Although elusive, this definition allows to bypass a critical question in the study of perception: does cognition influence perception? This is exactly what we do not want to do in this thesis that - instead - aims to contribute to fuel the debate concerning the problem of cognitive influence on perception.

This problem impedes to precisely define what is perception and is known as the problem of "cognitive penetrability of perception". It emerged from conflicting claims that, on the one hand, put forward that perception is not affected by cognition, and on the other hand, propose that cognition affects perception (Raftopoulos, 2001; Lupyan, 2017). From an adaptive point of view, both claims seem to be equally sensible: "An encapsulated perceptual system, kept separate from the influence of beliefs, could have the advantage of keeping our beliefs grounded in the truth offered by our senses. However, a cognitively penetrable perceptual apparatus may be equally adaptive, despite misperceiving and misbelieving, as long as the resulting behavior is adaptive." (Powers *et al.*, 2016). These last two decades, claims in accordance with the idea that cognition influences perception have flourished. A first argument in favour of perception penetrability concerns the fact that perception can at least be penetrated by cognition in an off-line (diachronic) way: experience and knowledge can induce changes in some patterns of intrinsic functional connectivity or even anatomical connectivity in the brain, resulting in changes in the way one will perceive in the future (Raftopoulos, 2001). A second argument concerns convincing cases of on-line (synchronic) perception penetrability (Lupyan, 2017; Raftopoulos, 2001; Zivony *et al.*, 2018; Powers *et al.*, 2016). For example, hallucinations can be considered as top-down cases of perception: no sensory information

is delivered to the organism, but the representation of a sensation (an hallucination) is cognitively constructed (Powers *et al.*, 2016). Still, the debate persists, as suggested by the numerous conflicting articles on this topic (e.g. Efron, 1969; Raftopoulos, 2001; Powers *et al.*, 2016; Lupyan, 2017; Zivony *et al.*, 2018).

A gateway towards the reinforcement of the claim according to which perception is cognitively penetrable is the study of attention, which has recently provided efficient arguments in favor of this claim (Lupyan, 2017; Zivony *et al.*, 2018). Attention has long been considered to be either a pre-perceptual (attention as a perceptual input selector) or a post-perceptual (attention as a formed-percept selector) cognitive process (Lupyan, 2017; Zivony *et al.*, 2018), somewhat leaving the issue of the cognitive penetrability of perception unresolved. However, experiments using bistable images suggested that the same perceptual input can be perceived in different manners, depending in the organisms' attentional states (Lupyan, 2017), which contradicts the view that attention is a pre-perceptual process consisting in selecting a given input. In addition, Zivony and colleagues (2018) showed that the high-level features of a second target (e.g. its semantic category) were poorly represented in working memory compared to its low-level features (e.g. its colors) during attentional blinks (impairment of a second target recognition if a first target has been presented just before). This implies that an attentional deficit (here, attentional blink) impairs perceptual processes (e.g. the perceptual representation of high-level features), thus disclaiming the idea that attention is a post-perceptual process. Together, these observations and theoretical insights place attention as a cognitive mechanism operating during perception (Lupyan, 2017). But, how does attention constraint perception? What makes it an ecologically useful function? The present thesis work attempts to address these questions and to better understand how attention operates, both at the behavioral and at the brain levels.

1.1 Cognitive psychology of attention

Organisms do not have unlimited physiological resources (Clark, 2003; Dukas, 2001; Dukas, 2004). On the other hand, the to-be-processed information coming from the external environment is nearly infinite. This poses a major problem. I previously introduced the ability of organisms to sense the world and suggested that this is of primary importance for their survival: if an organism receives more information than it can process, it becomes very probable that information relevant for its survival may be lost (e.g. food, presence of predators, etc), decreasing its adaptation to the environment (Clark, 2003; Dukas, 2004). However, this rationale holds true only when the processed information is sampled randomly from all available information. Indeed, by biasing perceptual processing towards behaviorally relevant items, or spatial locations, the organism can counteract the resources limitation, which is a main role of attention: attention

is a function that perceptively prioritizes certain features (feature-based attention) or portions of the space (spatial attention) according to their potential behavioral relevance (Corbetta & Shulman, 2002). Thus, attention can resolve the conflict opposing the need to process as much information as possible and the physiological restrictions precluding the processing of all the available information (James, 1995; Clark, 2003; Dukas, 2004).

This view of attention is one among a variety of attempts to define this concept, or subparts of it: divided attention, focused attention, selective attention, divided attention, involuntary attention, voluntary attention, spatial attention, feature-based attention, endogenous attention, exogenous attention, overt attention, covert attention, etc (Posner, 1980; Hommel *et al.*, 2019; Maquestiaux, 2017). However, it should be noticed that all these attempts call upon the idea that attention serves to select parts of information. In addition, Hommel and colleagues (2019) have recently alerted on the use of the term "attention", because it can entail so-called "confounds" both at the conceptual, behavioral and neural levels (e.g. concept of "intention"), leading to the conclusion that "no one knows what attention is" (Hommel *et al.*, 2019). To - at least partially - cope with the misuse of the term attention, a main advice in Hommel and colleagues' (2019) work is to use a synthetic approach that encompasses biological phenomena at different biological levels (development, evolution, cognition, neuroscience, psychology, ecology, etc) (Clark, 2003; Dukas, 2004). On several occasions in the introduction of the thesis, I alluded (and will allude) to findings in ecology and in evolutionary biology in order to follow this advice. This is why the definition of attention that I choose is voluntarily constructed on the basis of multidisciplinary works (Clark, 2003; Dukas, 2004; Hommel *et al.*, 2019). To pursue the attempt of following a multidisciplinary approach on the study of attention, a couple of fundamental questions needs to be asked. These are addressed in the next sections.

1.1.1 Highlighting the existence of attention

In his book "Principles of Psychology" (volume I) (James, 1995), William James defined attention as when the "focus of consciousness" is directed towards a particular item (a sound, an odor, a visual shape for example), and other items are "temporarily suppressed". In line with this, the Selective Attention Test of the Invisible Gorilla (see online video: <https://www.youtube.com/watch?v=vJG698U2Mvo&t=2s>, and see Simons & Chabris, 1999) assessed the ability of subjects to detect an unattended stimulus, while concurrently doing another task. The stimuli were videos where basketball players belonging to two teams (the white team and the black team) make passes. The participant's goal was to count the number of passes accomplished by one of the two teams. During this video, a gorilla unexpectedly crossed the screen. Strikingly, not all participants (range 8-83% of the participants, depending on the experiment parameters) were able to report the gorilla's presence. This accounts for

the fact that while focusing on details relevant for the current task (here the basket ball passes), people experienced a transient perceptual "blindness" that prevented them from noticing other (non-relevant) stimuli. Comparatively, in birds for example, the same phenomenon has been described, with limited attention constraining the ability to detect predators while looking for food (Dukas, 2004), reduced chances of target detection in the absence of cues (Dukas, 2001) and reduced chances of peripheral target detection during cryptic target trials compared to conspicuous target trials (Dukas, 2000).

Beyond visual attention, other paradigms such as the selective shadowing task in humans support the existence of attentional processing as a general, multimodal cognitive process: human participants have to repeat aloud an attended acoustic message while a supplementary unattended acoustic message is simultaneously played. When asked to report information about the unattended message, they poorly report (Driver, 2001). Again, at first glance, attention seems to be counterproductive with respect to the fact that it only offers a compromise between being perceptually infallible assuming remarkably high physiological costs and energy reserves, and being perceptually weak assuming low physiological costs and energy reserves (Clark, 2003). Yet, one should note that attention is hardwired (i.e. it emerges from physiological material) and that the synthesis of physiological material is not unlimited, thus making physiological compromises not particularly rare. An example of this is the way the human eye is designed: only the fovea (a small part of the retinal area) can receive and transmit visual information with a high accuracy (Clark, 2003). This obliges organisms to have a substantial gaze-shifting activity in order to perceive accurately stimuli at different locations. Attention embodies a similar compromise. Such compromises are always partially satisfying from a cognitive point of view, because they sometimes set aside potentially relevant information for the organisms' survival. Hence, they have to be extremely efficient to counterbalance these survival costs, attention making no exception. Note that, at this point, we introduce attention as a function that is totally aspecific with respect to the different sensory modalities, although we will then concentrate on visual attention.

1.1.2 Behavioral approach of attentional control

Whichever type of attention one is thinking of (implying saccades or not, being feature-based or spatial, etc), attentional control has been historically thought to be controlled in two distinctive ways (Maquestiaux, 2017; Corbetta & Shulman, 2002): 1) via so-called information contained within the stimuli themselves (e.g. their singular, distinctive colors, motions, sounds, etc); and 2) via so-called internal orienting goals (e.g. "an object one is looking for in his/her kitchen"). The first mechanism is referred to as exogenous attention, bottom-up attention or stimulus-driven attention; while the second is referred to as endogenous attention, top-down attention or goal-directed attention (Egeth & Yantis, 1997; Desimone & Duncan, 1995; Posner, 1980).

Experimentally, endogenous attention can be assessed by explicitly manipulating the participants' knowledge/expectations about the target. For example, the participant may be asked to discriminate whether the letter "A" is presented "right side-up" or "upside-down". In different trials, the target letter is presented on the left or the right side of the screen. In order to manipulate endogenous (spatial) attention, a cue can (cued displays) - or not (uncued displays) - precede the presentation of the target, indicating the left/right location of the upcoming target. Studies using such designs (e.g. Berger *et al.*, 2005; Goldberg *et al.*, 2001) found that the response times (RTs) in the spatially cued condition (when participants can voluntarily prepare to discriminate the target at the expected/cued location) are faster than RTs for targets in the uncued condition. These experimental results constitute a major evidence for the efficiency of endogenous attention in optimizing behavioral performance (see e.g. Ibos *et al.*, 2013, for analogous results in the non-human primate).

Concerning exogenous attention, one of the simplest evidence about how it can impact behavior is the visual pop-out search task. Here, the participant has again to discriminate a target (e.g. indicate the left/right orientation of a tilted bar, see figure 1.1), which can either pop-out (i.e. be easily identifiable because of its unique color, see figure 1.1B) or not (cf., figure 1.1.A). By comparing conditions where the target pops-out versus when it does not, one can control for the amount of endogenous engagement and measure the impact of the exogenous attention on behavioral performance. In pop-out trials, RTs are faster than in the non pop-out trials (Melloni *et al.*, 2012; Egeth & Yantis, 1997; Buschman & Miller, 2007).

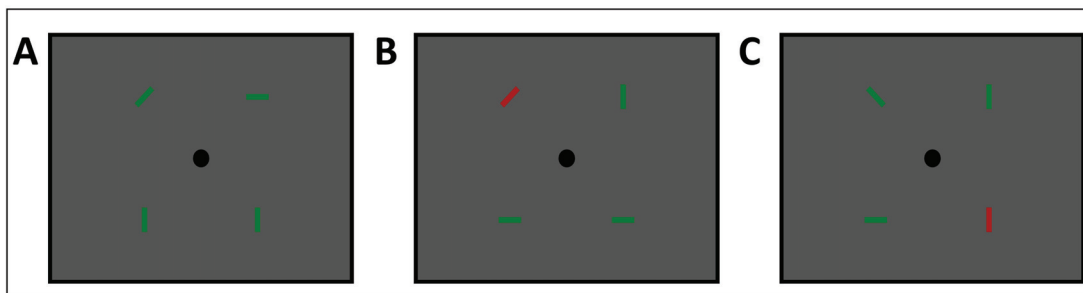


Figure 1.1: **Example of visual search displays**

A - Display with homogeneous stimulus saliency (all stimuli have the same color): the target is the tilted bar. Distractors are either horizontal or vertical. **B** - Display comprising a salient target (color singleton). **C** - Display comprising a salient distractor (color singleton).

Beside these definitions of endogenous and exogenous attention that may apply in a rather straightforward manner to simple stimuli and tasks (cf. figure 1.1), it should be stressed that in the real world such distinction may be more difficult to draw. Consider, for example, the natural images shown in figure 1.2. If asked to look for a mushroom (i.e. the target), subjects will make use of their prior knowledge about the visual features that make mushrooms distinguishable from other objects (e.g. "what visually differentiates the

mushroom from a snake, or a car, or a knife": its shape, its luminance, its texture, its color, its size, etc). One may argue that even in a situation where one has to look for a non-salient target (e.g. "the green mushroom among green plants"), the target has salient properties (i.e. "some features that the green mushroom does not share with the green plants": its texture, its shape, etc). This has been a major issue for teasing apart the contribution of endogenous and exogenous attentional signals (Egeth & Yantis, 1997). In the mushroom example, this would include capture by putatively exogenous signals (low-level physical features, such as curvatures) versus the contribution of endogenous knowledge about how (the very same) features characterize the target (i.e. the typical/expected shape of a mushroom).

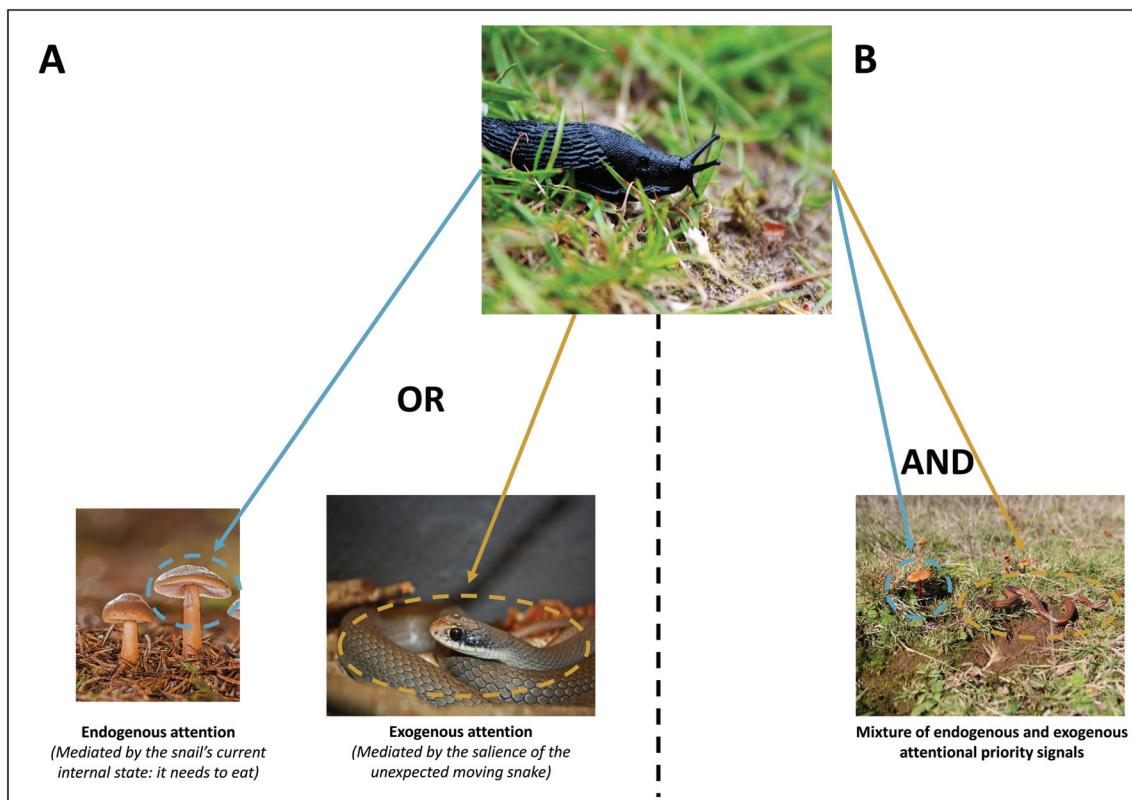


Figure 1.2: **Separate versus mixed contributions of endogenous & exogenous attention**

A - The separate description of endogenous and exogenous attention suffers from not taking into account the real-life configuration of sensory information. **B** - Real-life scenes contain mixtures of items that both endogenously and exogenously capture attention (see right panel).

Accordingly, from an ecological point of view, both types of signals are of primary interest and - most important - their joint effect of attentional selection should be carefully considered. If an organism is devoid of endogenous orienting abilities, it will, for example, not be efficient at identifying food. Conversely, if it is devoid of exogenous orienting abilities, it will, for example, not be efficient at identifying a dangerously approaching snake. Thus, presenting both abilities is needed to cope with environmental constraints: attentional focus can be set on relevant items according to internal states

(e.g. "attentional focus on mushrooms if the organism needs to eat") or on relevant items according to the state of its close environment (e.g. "attentional focus on the snake that is preparing to bite the organism"), see figure 1.2A. But can we expect that in real life conditions organisms always make use of either their endogenous attention or exogenous attention abilities (Macaluso & Doricchi, 2013)? In fact, organisms need to integrate information: for example, integrate information about "the mushrooms the organism needs to eat" and about "the dangerously approaching snake" (see figure 1.2B). The integration of multiple sources of information corresponds best with the definition of attention: attention biases perceptual processing abilities towards potentially behaviorally relevant items or spatial locations in the environment (e.g. Egeth & Yantis, 1997; Anderson, 2021, see the notion of "attentional priority").

But, what are the behavioral consequences of the presence of multiple attentional signals within the perceptual landscape? In figure 1.1A, I illustrate two types of spatial configurations: 1) the multiple signals relate to the same object and are congruent in space (i.e. the brown mushroom is both goal-relevant and salient, see figure 1.2A, left panel and see also figure 1.1B); or 2) the signals relate to different objects/regions of the space (the brown mushroom is the goal relevant object, but the snake movement produces the strongest stimulus driven signal, see figure 1.2B, and see also figure 1.1C). In the first scenario, the effects of the two signals (i.e. goal-relevance + color salience of the mushroom) jointly orient attention towards the same direction, inducing fast detection of the target. Experimentally, this corresponds to the pop-out displays described above and that consistently highlighted faster RTs when the target is also a salient singleton (compare displays on figure 1.1B versus 1.1A, cf. also Melloni *et al.*, 2012). Thus, the combination of the two attentional signals (goal-related target and stimulus salience) at a same spatial location boosts attentional performances.

The second scenario, when the attentional signals relate to different objects/locations, can entail several outcomes. The presence of multiple signals distributed across space raises the question of where attention is directed. One possibility is that attention is shifted sequentially between the different locations. This fits with the analogy of attentional orienting as being a spotlight that dynamically moves within the sensory landscape. A second possibility is that one of the two signals is given full priority, even leading to the suppression of the other signal (see "signal suppression hypothesis", below). The latter would imply that the organism is able to make an "attentional choice" between different stimuli having attentional signaling properties and competing for attention selection (Desimone & Duncan, 1995). The two mechanisms are not mutually exclusive and their relative contribution may vary as a function of the stimulus duration (long versus short duration of the co-occurring signals). In particular, the "attentional choice" account focuses on situations when the signals are available for a brief period of

time and it goes deeper in the details of how attention "chooses" relevant locations on a moment-to-moment basis.

Experimentally, the investigation of visuo-spatial attention shifting has first been operationalized using cueing paradigms. In the initial form of this paradigm (Posner, 1980), participants were informed that a target would appear on the right or on the left side of a screen. Shortly thereafter, the target appeared either in the cued location or in the opposite one and participants had to indicate as fast as possible when they detected the stimulus. The cue was 80% predictive of the actual location of the target. RTs were shorter in valid cueing condition than in invalid cueing condition (Posner, 1980). The cueing paradigm highlights to what extent attention is a dynamic function: the cueing phase, which constitutes the first of the two attentional signals, biases attentional control towards one side of the screen. This in turn makes it more difficult to detect stimuli located on the other side, because attentional control needs supplementary operations to re-orient towards the location of the (invalidly cued) target. Using a similar paradigm, Folk and colleagues (1992) suggested that attentional shifts elicited by invalid cueing of the target position were dependent on the perceptual relationship between the cue and the target. Folk and colleagues (1992) made use of a cueing paradigm, but this time the target could appear in one of four spatial positions. Another difference with the initial cueing paradigm (Posner, 1980) was that Folk and colleagues (1992) independently manipulated the perceptual relationship between the cue and the target: the cue could either be a color singleton or an abrupt onset singleton, and so was the target. They found that the behavioral costs elicited by invalid cueing of the target location only take place when the cue and the target perceptual properties are linked (e.g. both are abrupt onsets or color singletons). They concluded that invalid cueing elicited attentional shifts only under these specific conditions: that is, when there was some similarity between the perceptual properties of the cue and the target. This work has led to a new account called the "contingent involuntary orienting hypothesis" and has been highly influential (Folk *et al.*, 1992). We will see that it has many implications on the theoretical construction of the following sections, but while it accounts for the properties of the dynamic nature of attention by pointing out the conditions under which attentional shifts occur, it does not completely explain how attentional orienting occurs at one given moment in the presence of multiple item having attentional signaling properties.

By contrast, the case of the so-called "attentional choice" is rooted in the fact that sensory landscapes are composed of multiple, co-occurring items that compete for attentional processing/selection (Macaluso & Doricchi, 2013). The challenge being to rapidly select the behaviorally-relevant stimuli, by evaluating all stimuli in the sensory landscape and figuring out whether they are task-relevant stimuli or task-irrelevant distractors. This is where the situation gets dramatically intricate: how does attention

"choose" between all the attentional signals in a moment-to-moment manner (Desimone & Duncan, 1995)? From a behavioral point of view, just similarly to the invalid cueing condition I detailed in the previous paragraph, the presence of a target to be detected accompanied by the presence of a task-irrelevant but salient distractor (see figure 1.1C) makes the detection of the target more difficult, with increased RTs and error rates compared to a control condition with no salient distractor (e.g. Melloni *et al.*, 2012; Ferrante *et al.*, 2018). In that situation, behavioral data suggest that the attentional computation underlying the target detection is less straightforward in the presence of competing attentional signals than when a single attentional signal is present. However, there are situations similar to the one just described where behavioral performances are surprisingly high even in the presence of a salient distractor.

In fact, the "contingent involuntary orienting hypothesis" (Folk *et al.*, 1992) has accurately described some of the boundary conditions controlling attentional orienting, in particular stressing the central role of the current task demand (Luck, Gaspelin, *et al.*, 2021). Nonetheless, three decades after the framing of this hypothesis, the debate is unresolved and alternative accounts have been put forward. For instance, according to the "signal suppression hypothesis" (Luck, Gaspelin, *et al.*, 2021; Gaspelin, Leonard, *et al.*, 2017; Geng, 2014), a central function of attention is to "suppress" salient task-irrelevant items (Geng, 2014). This would enable reducing the interference between task-irrelevant and task-relevant items. This suppression mechanism can be proactive (i.e. the suppression is done in knowledge-based anticipation of sources of distraction/task-irrelevance) or reactive (i.e. the suppression is done "online" in the presence of task-irrelevant items that could not be proactively suppressed). Both mechanisms tend to work in synergy towards the most adaptive behaviors (Geng & DiQuattro, 2010; Geng, 2014). Suppression, for example, happens if participants are told to look for a target of a specific shape (known in advance by the participants) in a visual display, which also includes a color singleton that is never the target, as well as other shape singletons (Gaspelin, Leonard, *et al.*, 2017). The main interest of such search conditions is to avoid any "singleton detection strategy" that is likely to take place when the display contains a singleton target along with non-singleton distractors (see figure 1.1: the target bar is the only tilted bar; see Gaspelin, Leonard, *et al.*, 2017). In such search conditions, where the target cannot be detected solely on the basis of its pop-out features, the participants produce less saccades towards the task-irrelevant color singleton than towards the other (non-salient) distractors also present in the visual display (Luck, Gaspelin, *et al.*, 2021; Gaspelin, Leonard, *et al.*, 2017). Moreover, the presence of a color singleton does not yield to any decrease of behavioral performance compared with homogenous displays without any color singleton (Gaspelin, Leonard, *et al.*, 2017).

In sum, there is extensive evidence that different types of signals can affect behavioral performance. These can be generally classified as endogenous (pertaining to internal goals and expectations) versus exogenous signals (referring to physical properties of the stimuli). Importantly, an in-depth understanding of the functioning of the attention control requires considering how these different signals interact with each other when presented concurrently, as it happens in any real world situation. While behavioral experiments provide us with important insights about such interactions, they cannot give us any information about how these signals may interact at the different stages of the visual processing cascade. In line with this, Anderson (2021) proposed a framework that considers attentional control as being the result of multiple computations taking place in different brain areas. Thus, attention should be studied using multiscale approaches (e.g. coupling brain and behavioral investigations) going beyond long-lasting debates around dichotomies in attentional control (e.g. "does that specific stimulus capture attention or not?"). This is the approach that I followed in my thesis, and a main objective of this thesis work. In the next sections, I will first present an overview of the organization of the visual system and then move to reviewing mechanisms of attentional control.

1.2 Functional organization of the visual system in the brain

The processing of visual signals starts with light arriving at the retina - the inner layer of the eye - that is made of photoreceptors. There are two types of photoreceptors: rods (mainly specialized in color processing and high-resolution vision) and cones (mainly specialized in light sensitivity). When light attains these specialized cells, the different light-sensitive channel receptors at their surface modify their configuration compared to dark conditions. Some receptors become porous to ions, while others conversely close. This induces a change in the membrane potential of the photoreceptors, which, as in typical models of neuronal cell communication, causes a change of released neurotransmitter quantity at the post-synaptic level. The cellular circuitry receiving information from the photoreceptors for further processing allows the ganglion cells to adapt their electrophysiological activity as a function of the amount of light and the shape of a stimulus falling within their receptive field. This, in turn, is responsible for the fine-tuned early processing of the visual scene (Purves, 2008). Once the visual information has travelled through this primary cellular circuitry, it is centrally processed by different types of neurons that are specialized for various types of visual information: motion, color, contrasts, etc. This information circulates from the retina to the central nervous system through the optic nerve, the whole set of axons of the ganglion cells. The axons reach the optic chiasm, where a fraction of the axons projects contralaterally, while the other fraction projects ipsilaterally. In majority, the axons project to the geniculate nucleus of the thalamus or to the superior colliculus. The axons of the geniculate nucleus' neurons then reach the occipital cortex.

The occipital cortex is subdivided into main hierarchical areas that differ in their main visual functions and the neurons of each of these areas can be compared as workers that have a very specific task within a production line. In the end, the result of all these specific tasks is a precise, colored, high definition visual perception, albeit the processing of visual information begins before the information reaches the occipital cortex (e.g. in the eye itself). Here I will go deeper in the anatomo-functional details of the occipital cortex because this is a brain region of major interest in this thesis. To do so, I first borrow a fundamental question: "what must the [occipital] cortex accomplish?" (cited from Deyoe in Ramachandran, 2002). This question is of primary interest here because it pushes into considering all the information that should and could be extracted and transformed from the light patterns getting the eye in order to compute an efficient representation of the visual scene. Light patterns are primarily defined by their spatial, temporal, intensity and wavelength features (Ramachandran, 2002). First, a particularly important feature of (but not specific to) the visual system is the spatially coherent organization of the visual information processing. In fact, the spatial configuration of

the visual field is authentically maintained in the brain, thus constituting a brain spatial mapping of the visual field (except that spatial locations are centrosymmetrically inverted, which is a matter of where the light of a given part of the visual field projects to the retina). This means that the top-left part of the visual field is, for example, represented in the bottom-right part of the occipital cortex. This is called the retinotopic representation of the visual field (Purves, 2008; Ramachandran, 2002; Engel, 1997) (see figure 1.3A) and it is shared by all regions of the occipital cortex. However, the size of the receptive field of the neurons across the visual areas increase with their position in the visual hierarchy (Ramachandran, 2002; Dumoulin & Wandell, 2008; Engel, 1997; Yantis, 2005), which is related to their function as part of the visual hierarchy (i.e. from the coding of very basic features of a visual scene to the complex objects categorization or face discrimination).

The first area of the occipital cortex that receives inputs from the lateral geniculate is the primary visual cortex, also referred to as the striate cortex (V1, Brodmann area 17). The role of V1 neurons has initially been determined while trying to understand the relation between stimulus features and neuronal responses in the cat's primary visual cortex (Hubel & Wiesel, 1959; Purves, 2008). Hubel & Wiesel (1959) found that the most efficient stimuli to trigger the firing of these neurons were oriented bars. Depending on the neuron, the orientation of the bar that activated the neuron most effectively was different (e.g. some neurons responded to vertical bars, and not to 45°-tilted bars, while the reverse happened in other neurons). This suggested that, on top of exhibiting retinotopically-specific responses, the V1 neurons also showed response patterns specific to the orientation of the visual stimuli. So far in the visual processing then, the orientation of the stimuli is the main feature that is decoded, which gives simple information about shapes and contours (Purves, 2008; Ramachandran, 2002) as a function of the location, that is, global information about the visual scene. Actually, most, if not all, visual scenes comprise edges, orientations variations and contours, which implies that V1 neurons are involved in virtually any visual stimulations (Ramachandran, 2002). This is also the case for V2 (note: most occipital areas are classified starting from the primary visual cortex: V1, V2, V3, V4, etc) neurons (Brodmann area 18), that are also selective for contours and edges. However, V2 and V1 are functionally different in that V2 neurons can for example process illusory information (e.g. illusory edges): in tasks involving the passive viewing of illusory edges, V2 neurons respond reliably to the illusory edges, which is not the case for V1 neurons (Ramachandran, 2002). Starting from V3 (part of Brodmann area 19), neurons are selective to visual features such as luminance-based contours and motion. The description of specific deficits following lesions of "higher" visual areas such as V4 (part of Brodmann area 19) and V5 (also part of Brodmann area 19) has allowed to further understand the next steps of the processing hierarchy. For example, patients with a lesion in area V4 suffer from achromatopsia (Purves, 2008): they cannot perceive colors anymore.

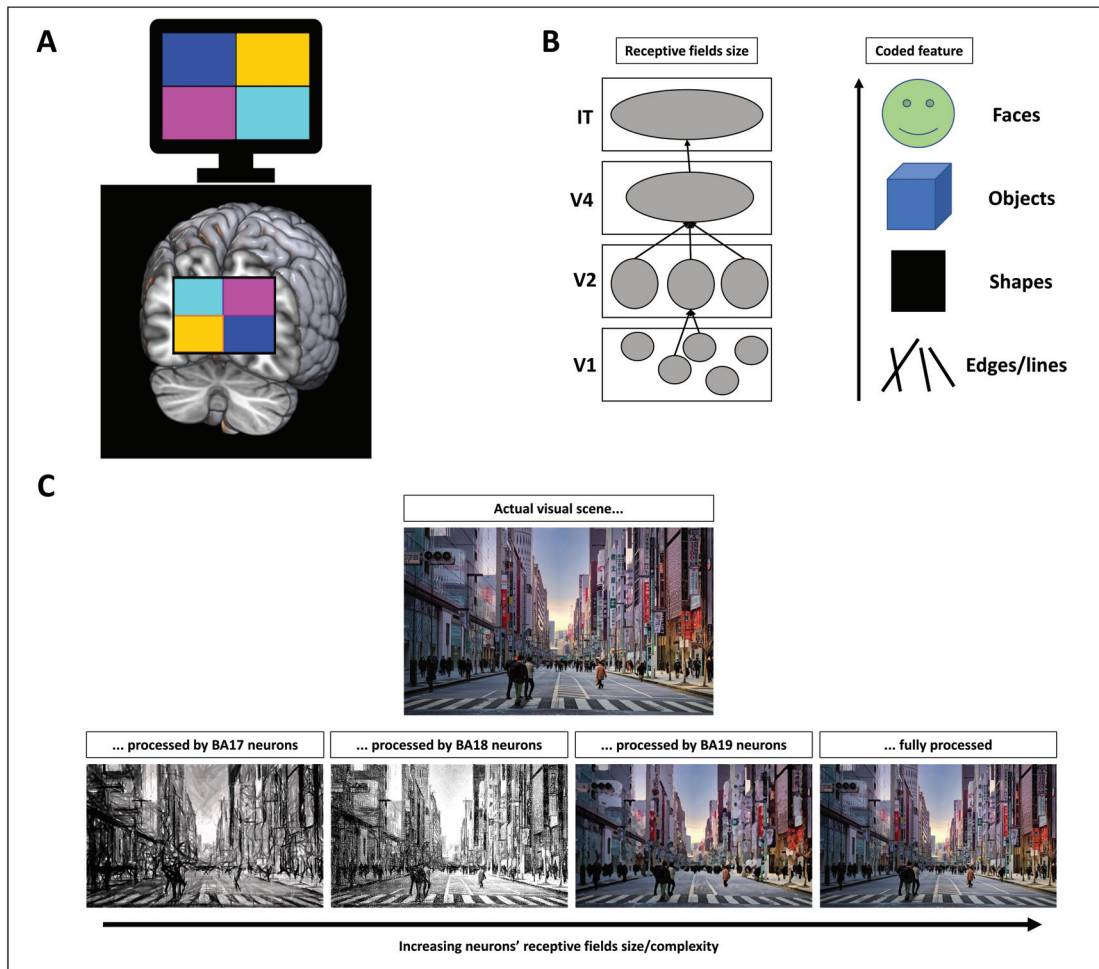


Figure 1.3: **Organization of the visual system**

A - Schematic illustration of the retinotopic representation of the visual field in the occipital cortex. Imagine one is fixating the center of a screen (see top panel). If, while he/she keeps fixating, we input a visual stimulation in the top-left quadrant of the screen, the neuronal response to this stimulation will be located in the bottom-right part of the occipital (see bottom panel). This, of course, applies to all other three quadrants. **B** - Organization of the receptive field size and of the features coded along the visual hierarchy. **C** - Illustration of the hierarchical processing of a visual scene (adapted from Yantis, 2005). As the visual information progresses through the hierarchy of the visual brain, neurons increase in their response complexity/specificity (from orientation discrimination in the striate cortex (BA17) to faces recognition in the fusiform face area). The images customization as been done using PowerPoint basic image modification options. Thus it does not accurately represents how a given visual scene is perceived through the visual hierarchy. BA = Brodmann Area.

In these patients, the cones configuration in the retina is intact: the problem comes later in the visual processing, with V4 neurons being absent/non-functional. Hence, V4 neurons are crucial for color perception. Similarly, lesions in the V5 area cause cerebral akinetopia: patients with such lesions have difficulties with motion processing. In sum, the occipital cortex neurons partially work in a partitioned, sequential manner so that in the end we are able to see what we see (Purves, 2008; Ramachandran, 2002). This

sequential processing of visual information by neurons functionally specialized in the coding of increasingly complex stimulus features, as well as the increasing size of the neuron's receptive fields along the visual hierarchy, make stimuli distinguishable from each other (figure 1.3B and C). Thus, the synergetic functioning of the multiple visual areas is the source of the integration of all visual information and the estimation of their task relevance (identification, recognition, etc; see Ramachandran, 2002).

Importantly, visual scenes in the real world are more complex than single oriented bars or light spots exactly falling at the center of a given neuron's specific receptive field (Purves, 2008): in fact, there are often multiple stimuli that fall into the receptive fields of different neurons. Further, the stimuli are different from each other, making the visual neurons more or less responsive to one or another stimulus. Chelazzi and colleagues (1998) tested the effect of presenting multiple visual stimuli at the same time, within the receptive field of single neurons in the inferior temporal cortex (IT: an area contributing to object recognition, as part of the ventral visual stream). Electrophysiological recording was done in monkeys. The stimuli were either: i) an "efficient" stimulus, eliciting an optimal response of the stimulated neuron; or ii) an "inefficient" stimulus, eliciting a weak/an absence of response of the stimulated neuron; or iii) both types of stimuli presented at the same time, within the neuron's receptive field. The goal of the study was to investigate the competition taking place in the presence of more than one stimulus in the neuron's receptive field, with attention kept constant across the three experimental conditions. To do so, Chelazzi and colleagues (1998) used a search task with "target absent" trials, during which monkeys were first cued to attend a specific stimulus object (e.g. a cherry) that they would have to look for in a second step of the trial. The cue object was actually always absent in the stimulus display (containing one or two object stimuli, e.g. a mug, or a mug and a flower) following the cueing phase. They found, as expected, that the inefficient stimulus presented alone elicited less neuronal activity (i.e. number of spikes per second) than the efficient visual stimulus presented alone. The main result of the study was that the presentation of the two visual stimuli at the same time elicited an intermediate level of activation: it was not as high as when the efficient stimulus was presented alone, but not as low as when the inefficient stimulus was presented alone. This provides us with a possible physiological signature of competition at the single neuron level, when the visual system is presented with multiple stimuli at the same time.

1.3 Attentional control in the brain

1.3.1 The biased competition model

In the previous section I pointed out that occipital neurons are specialized in responding to particular stimuli features (their orientation, their shape, their color, etc) (Purves, 2008) and - most important - that the presence of multiple stimuli in the visual field can lead to sensory competition at the neurophysiological level (Chelazzi, Duncan, *et al.*, 1998). However, bringing attentional control into the equation makes the whole story far more complex. Early evidence for such complexification dates back to Moran & Desimone (1985), who measured monkey occipital (V1 and V4), and IT cortex single neurons' responses to visual stimuli falling within their receptive field while manipulating attention to those stimuli. The visual display contained a fixation dot plus two stimuli placed within the receptive field of a specific neuron: one of the stimuli was "efficient" in this sense that the neuron responded to it, while the other stimulus was "inefficient", because the neuron did not respond to it. Hence, the sensory conditions remained exactly the same throughout the entire experiment. In a subset of trials, the monkey was trained to attend to the efficient stimulus, while in another subset of trials attention was directed towards the inefficient stimulus. Gaze was maintained on the fixation dot. The authors found that when the monkey attended to the efficient stimulus, the neuron's responses were not attenuated compared to its responses to this same stimulus with no attention drawn towards it. At variance, when attention was directed towards the inefficient stimulus, then the neuron's responses were attenuated compared to its responses to the efficient stimulus with no attention drawn towards it. This last effect was observed when both the efficient and the inefficient stimuli were presented within the recorded neuron's receptive field. To control whether this effect could be generalized to the situations when the stimuli are in the receptive fields of different neurons, the authors repeated the experiment with only the following change: the efficient stimulus was presented in the recorded neuron's receptive field, while the inefficient stimulus was placed outside of it. In different conditions either the efficient or the inefficient stimulus was attended. The neuron's response to the efficient stimulus was similar in the two conditions, indicating that attention modulates the neuron's response, but only when there are two competing stimuli in the neuron's receptive field.

This study constitutes one of the first evidence supporting what will later be referred to as the biased competition model - basically stating that the sensory competition occurring between the brain representations of multiple stimuli can be biased by attention (Desimone & Duncan, 1995; Desimone, 1998b). Nonetheless, because these neurophysiological findings apply only when the two stimuli fall within the receptive field of the same neuron (Moran & Desimone, 1985), they cannot easily explain many effects reported in behavioral and brain studies (Luck, 1995; Luck, Chelazzi, *et al.*, 1997; Desimone & Dun-

can, 1995). For example, the size of a visual search array (where the stimuli are not all in a single neuron's receptive field) increases the time that participants need to find/select the target (e.g. see Desimone & Duncan, 1995). Further, visual attentional capture can occur across the entire visual field, not only across a single neuron's receptive field (Luck, Chelazzi, *et al.*, 1997; Moore & Armstrong, 2003; Yantis, 2005). For example, Luck (1995) showed that an electroencephalography (EEG) component, known as "N2pc" and typically observed during attentional tasks, was observed when a target had to be found among distractors scattered across the whole screen, but was absent when the target was presented alone.

In a later study, Luck and colleagues (1997) confirmed most of the results of Moran & Desimone (1985) about attentional effects for stimuli presented either within the same receptive field or different receptive fields, but their conclusions were nuanced. While they used similar recording and visual stimulation methods as in Moran & Desimone (1985), Luck and colleague (1997) could observe baseline shifts of firing rate of neurons whose receptive fields included the attended location, even when no visual stimulus had been presented yet. These shifts were observable irrespective of whether the stimulus that would appear at the attended location thereafter was an efficient or inefficient stimulus. These results highlight that attention can prioritize processing at specific location of the space by enhancing their brain representations. Thus, rather than supporting the notion that biased competition only occurs at the level of the single neuron's receptive field, these observations suggest that competition also occurs on a larger scale, accounting for the selection of specific/attended spatial locations in the visual field. Thus, the *prima facie* contradiction (competition between stimuli only at the local/within-receptive field level, see Moran & Desimone, 1985, versus at the global/whole visual field level, see Luck, 1995) between the results of single-cell recording studies and from EEG and behavioral studies may reflect specific methodological characteristics of these different methodologies (Duncan, 1998).

Early studies that contributed to formalize the biased competition model (e.g. Moran & Desimone, 1985; Luck, Chelazzi, *et al.*, 1997; Chelazzi, Duncan, *et al.*, 1998) have mostly focused on the relationship between attention and neuronal responses to competing visual stimuli, that is, how a given internal attentional state biases the sensory competition. Such manipulation of internal attentional states refers to the study of endogenous attention. In the "Behavioral approach of attentional control" subsection, I mentioned that visual attention makes use of the internal states of the organism, as well as the exogenous physical characteristics of the stimuli in order to prioritize items/regions of the space in an efficient manner. Behavioral data show that salient targets are easier to find than non-salient targets (Melloni *et al.*, 2012; Desimone & Duncan, 1995), which suggests that the biasing of the sensory competition can occur even when the internal (endogenous) state is kept constant, and this is thought to be salience-driven (see Yantis, 2005). Does any such exogenous mechanism works the same way as the so-called endogenous attention

mechanism, that is by gating the responses of occipital neurons?

Reynolds and colleagues (2003) used a similar methodology as Moran & Desimone (1985) and Luck and colleagues (1997), but this time they manipulated the contrast of a given visual stimulus to test its effect on single neurons' responses of the occipital cortex. They displayed two stimuli in the receptive field of a single occipital neuron, while asking the monkey to attend to another stimulus, placed outside of the neuron's receptive field. One of the stimuli was known to elicit robust responses of the neuron, and hence was considered the efficient stimulus. Its contrast was fixed. The other stimulus was known to elicit poor responses of the neuron (considered an inefficient stimulus) but its contrast varied across trials. The hypothesis made by Reynolds and colleagues (2003) was that the higher the contrast of the inefficient stimulus, the more the neuron's response would resemble the one of the inefficient stimulus presented alone. On the contrary, the weaker the contrast of the inefficient stimulus, the more the neuron's response would resemble the response associated with the efficient stimulus presented alone. In other words, increasing the contrast of the inefficient stimulus was hypothesized to make it "more competitive" compared to the efficient stimulus. This is indeed what they found, confirming that stimulus salience can bias the sensory competition between stimuli towards the most salient stimulus.

Although there is no theoretical reason to doubt that this "salience-driven" attentional effect can occur beyond the single receptive field scale, Reynolds and colleagues (2003) only showed that it occurs at the level of the receptive field. Single-cell recording has paved the way of the understanding of the brain mechanisms involved in attentional control, notably by substantially contributing to the formalization of the biased competition model (e.g. Moran & Desimone, 1985; Desimone & Duncan, 1995; Luck, Chelazzi, *et al.*, 1997; Chelazzi, Duncan, *et al.*, 1998; Reynolds & Desimone, 2003). Nonetheless, it suffers from being focused on the response of one or a few neuron(s), impeding the study of the biased competition at larger scales. Functional magnetic resonance imaging (fMRI), a method based on the measurement of the brain haemodynamics (see Method section, at the end of the Introduction), allows to study biased competition mechanisms at the level of the whole brain. In particular, fMRI studies have been conducted in order to test the predictions of the biased competition model, specifically concerning salience-driven, exogenous attention in the occipital cortex.

In a human fMRI study, Beck & Kastner (2005) investigated visuo-spatial attention control crossing two experimental factors with two levels each. The visual display included a set of stimuli presented in the top-right visual quadrant. The first factor was the grouping of the stimuli in time, that is, whether the stimuli were presented in a simultaneous (four stimuli at the same time in the top-right screen quadrant) or in a sequential (the four stimuli presented one at a time in the top-right screen quadrant) manner. The second factor was whether the display contained a pop-out stimulus, plus three identical

ones, or four stimuli all different from each other (heterogeneous display). This resulted in a total of four experimental conditions: 1) heterogeneous display with stimuli presented sequentially, 2) heterogeneous display with stimuli presented simultaneously, 3) pop-out display with stimuli presented sequentially and 4) pop-out display with stimuli presented simultaneously. The authors first computed a sensory suppression index, comparing sequential trials versus simultaneous trials. This index was significantly greater than zero in areas V2 and V4 for the heterogeneous display. They then compared this index values between the heterogeneous display and the pop-out display. The prediction was that the competition would be weaker for the pop-out display compared to the heterogeneous display due to the bias in favor of the pop-out stimulus (Reynolds & Desimone, 2003), and this should result in a smaller sensory suppression index for the pop-out display compared to the heterogeneous display. This is indeed what they observed in areas V2 and V4. In area V1, this index was even negative for the pop-out display, and this was interpreted as the fact that V1 could be the source of the pop-out bias observed in the higher-order areas.

In sum, Beck & Kastner (2005) highlighted that pop-out visual stimuli can trigger a bias towards their representation at the level of the occipital cortex, making the competition "resolved" between the occipital representations of the visual stimuli. In a similar fMRI study, Kastner and colleagues (1998) investigated the role of endogenous (goal-directed) attention on the occipital responses. As in Beck & Kastner (2005), there were two experimental factors with two levels each. The first factor was the grouping of the stimuli in time (simultaneous versus sequential presentation of the four stimuli in the top-right quadrant). The second factor was the spatial direction of endogenous attention, that is, whether the participants were asked to perform an attentional task at central fixation ("display unattended" condition), or they had to perform a task by covertly attending to the visual stimuli ("display attended" condition). In order to assess the effect of endogenous attention on the sensory suppression, they compared the sensory suppression index (described above) for the attended versus unattended condition. Comparably to the results found in Beck & Kastner (2005), Kastner and colleagues (1998) found that the sensory suppression index was significantly lower for the "display attended" compared with "display unattended", both in V2 and V4.

Using similar methodologies, these two studies show that endogenous and exogenous attentional bias have similar signatures, as measured using human fMRI. In another human fMRI study, Kastner and colleagues (1999) used the same methodology and display types, except that they included - on a trial-by-trial basis - a cueing signal indicating to the participants that the visual stimulation was going to be displayed in the relevant, top-right quadrant. The relatively long period of time between the cue and the display onset allowed them to measure the signal reflecting the preparation for the displayed stimulation. In other words, this study was designed to observe the effect of covertly attending (due to the cue) a region of the space in the absence of visual

stimulation. Consistent with results of Luck and colleagues (1997), who showed baseline increases of neuronal firing when monkeys were cued to attend to a given stimulus, Kastner and colleagues (1999) found increased activity in the occipital cortex representing the screen region where the visual stimulation was expected to be displayed. Thus, in addition to prioritizing processing of the incoming sensory input (either related to salience, exogenous attention; or to current task-goal, endogenous attention), attentional control can bias the activity of the occipital cortex even in the absence of visual signals. This indicates that there are important properties relating to how attentional signals spread through time and suggests that prior experience/expectations can play a crucial role in attentional control.

From the results discussed above, we learn that activity in the occipital cortex does not only depend on the capacity of visual stimulations to trigger the response of a specific neuron, but it also depends on what stimulus is attended within arrays containing multiple stimuli (Moran & Desimone, 1985; Luck, Chelazzi, *et al.*, 1997; Kastner, De Weerd, Desimone, *et al.*, 1998). This means that the sensory competition taking place in the presence of multiple stimuli can be biased, so that one of the items is attentionally selected/chosen for further processing: hence, the "biased competition model". As detailed in the "Highlighting the existence of attention" section, the biased competition model posits that two main factors bias the competition towards the processing of specific stimuli: their pop-out features and their relation to the organism's goals (Desimone & Duncan, 1995). Of note, early studies related to the biased competition model have focused on the responses of neurons in the occipital cortex. This precluded the understanding of the possible contribution of other, higher-order regions that may have a role in generating the attentional biases. In the next section I will address this by considering areas in the frontal and the parietal cortex that are considered key players in attention control.

1.3.2 The frontoparietal attentional network

At this point, we considered "attention" as being a driving force for the modulation of neuronal responses in the occipital cortex. However, the term "attention" cannot mechanistically explain what elicited the changes of activity in the occipital cortex. On the basis of their results obtained on occipital neurons recording, Chelazzi and colleagues (1998) proposed a simple model of visual attentional control. They reasoned that in their study, but also in general during attentional tasks, the selection of the target was not performed on the basis of the specific properties of the target stimulus per se (e.g. the pop-out physical properties of the target compared to other stimuli), but rather via some interaction between the target's physical properties and an "internal idea of what the target is/resembles". In other words, attentional selection might be due to some matching between the properties of a stimulus and a "target template" of the to-be-selected stimulus. They proposed that working memory (i.e. keeping in mind some

information while performing a task, e.g. see Baddeley, 2010) may play a role in the formation of the target template and in matching it with the current visual inputs, with a significant contribution of (pre)frontal areas (see Miller *et al.*, 1996 for such evidence using a similar task as in Chelazzi, Duncan, *et al.*, 1998).

Chelazzi and colleagues' (1998) model of visual attentional control involved prefrontal cortex's and IT neuron's, although they did also mention a possible role of other frontal areas such as the frontal eye field (FEF). The model posits that at the beginning of a visual search task trial, all neurons of the IT cortex have the same baseline activity (see figure 1.4). During the following cueing phase, IT neurons specifically coding the cued feature (e.g. a red square) increase their activity, while inhibiting the neighboring neurons that do not code for the relevant feature. During the delay period, all IT neurons go back to their baseline activity, because there is no visual stimulation. At the same time, the prefrontal cortex "keeps in mind" (working memory) the information relative to the target (target template), and starts to bias the activity of the IT cells specific to the cued stimulus, in preparation to the stimulus array presentation. The stimulus array phase first triggers the increase of activity of both neurons specific to the cued stimulus features (the red square in figure 1.4) and to the distractor (the green square in figure 1.4), but the bias sent by the prefrontal cortex to the IT neurons specific for the cued feature makes the activity of the relevant neurons more sustained. Concurrently, these relevant neurons inhibit the IT neurons that are not specific for the cued feature, making their activity close to baseline (cf. figure 1.4). In this framework, prefrontal control allows selective biasing of the IT neurons representing the attended stimulus/feature, while inhibiting the other neurons.

Although theoretically very important, Chelazzi and colleagues' (1998) model needed some formal testing because visual attention was mainly conceived in terms of driving function, rather than in terms of brain structures areas, most likely due to methodological limitations and indirect testing (e.g. lesion studies, occipital monkey electrophysiology, see Duncan, 1998, for a discussion). Moore & Armstrong (2003) made use of a similar electrophysiological experimental strategy as in Moran & Desimone (1985), Luck and colleagues (1997) and Chelazzi and colleagues (1998). They made the hypothesis, related to Chelazzi and colleagues' (1998) model, that FEF neurons contribute to bias occipital responses, critically contributing to the mechanism of attention control (see also Tehovnik *et al.*, 2000, cited by Moore & Armstrong, 2003). Moore & Armstrong (2003) recorded monkey V4 neurons' activity during a visual task while manipulating: 1) the visual display configuration, and 2) the monkey's FEF activity using electrical subthreshold stimulations. They first observed that efficient stimuli elicited a significantly larger response (firing rate) of the V4 neurons, compared to baseline with no visual stimulation (similar to Moran & Desimone (1985), Luck and colleagues (1997) and Chelazzi and

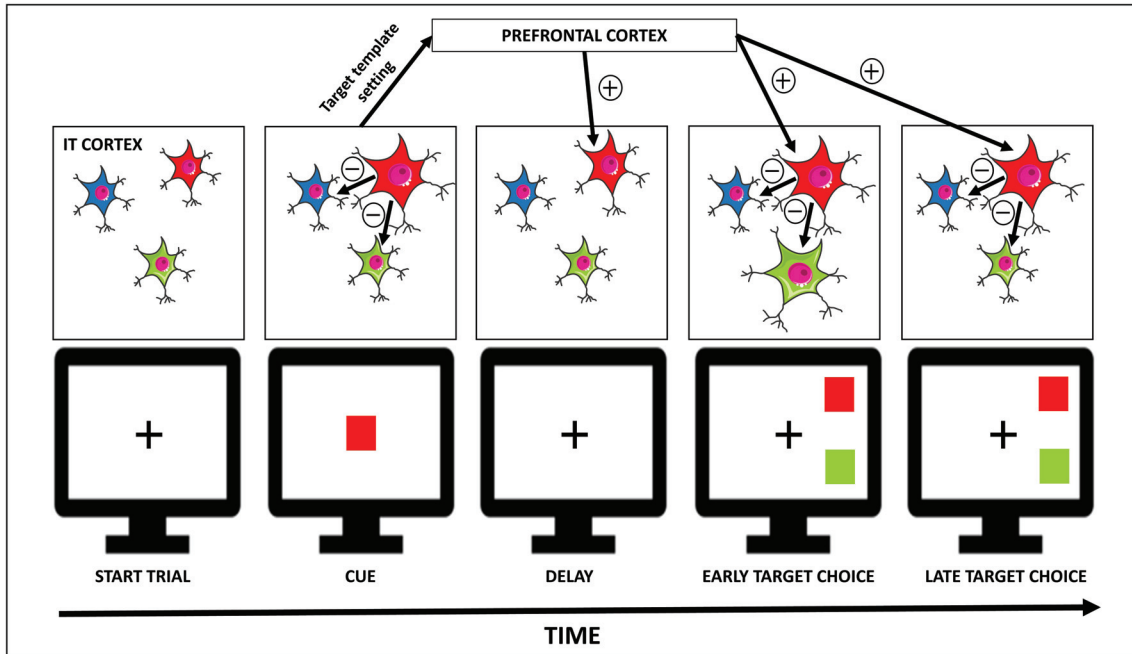


Figure 1.4: **Schematic representation of the activity of IT cortex neurons during a visual search task (adapted from Chelazzi, Duncan, *et al.*, 1998).** The boxes containing the neurons are a schematic representation of the IT cortex. At each step of the visual search task trial (the screens represent what is displayed during each step), the size of the neurons represents their firing rate. The neurons' color represents their stimulus specificity (e.g. the red square efficiently drives the red neuron's response). The arrows, accompanied by a "+" or a "-", represent the modulatory exciting/inhibiting effects between neurons/brain structures.

colleagues (1998)). Next, they stimulated FEF neurons which triggered a saccade to the same retinotopic coordinates as the V4 recorded neurons, but in a subthreshold manner so that the saccade does not occur. By doing so, they knew that the FEF neurons' activity matched the V4 recorded neuron's activity in terms of retinotopic coordinates. In the condition comprising both visual stimulation (stimuli on the display) and FEF stimulation, they observed that the V4 neuron's response was larger than visual stimulation condition without any FEF stimulation. In addition, when doing exactly the same comparison, but this time with an inefficient stimulus, they observed the same difference: the V4 recorded neuron's response to the inefficient stimulus was higher during FEF stimulation than with no FEF stimulation. When there was no visual stimulation, the FEF subthreshold stimulation had no effect on the V4 neuron's activity.

These results suggest that FEF stimulation can enhance occipital neurons' activity only in the presence of visual stimuli. In a second experiment, they placed a visual distractor outside the V4 neuron's receptive field, in addition to the target that was inside the receptive field. The effect of the FEF subthreshold stimulation was larger when the visual distractor was present outside the receptive field than when it was absent. This suggests that in visual displays containing multiple visual stimuli, the FEF exerts a bias towards the neurons representing the target stimulus, even when the distractor is

outside of the neuron's receptive field. In a last experiment, Moore & Armstrong (2003) used the same visual display as in the previous experiment, but now they subthreshold-stimulated FEF neurons known to trigger saccades towards the distractor location. The results showed that the FEF subthreshold stimulation now reduced the activity of the V4 neurons representing the target stimulus. This highlights that the FEF involvement in biasing activity in the occipital cortex applies even across neurons with non-overlapping receptive fields. In fact, the FEF subthreshold stimulation appears to mimic the attentional selection of a specific stimulus, having a suppressive effect on the V4 neurons' representing the distractors.

From this study, we learn about three crucial features of attentional control: 1) the FEF is involved in the so-called "attentional effect" (described in Moran & Desimone (1985), Luck and colleagues (1997) and Chelazzi and colleagues (1998) for example) and it contributes to enhance the response of occipital neurons that represent the target stimulus; 2) the selection bias for a specific stimulus/region of the visual space is more pronounced in the presence of a distractor, even when this is presented outside of the receptive field of the neuron that represents the target; 3) the attentional selection bias does not only enhance the activity associated with the target, but also suppresses the activity of neurons representing non-selected stimuli/locations. These findings fit with the predictions of the model proposed by Chelazzi and colleagues (1998), but several questions remain unanswered. For example, are frontal areas the only brain regions contributing to the biasing of the occipital cortex activity? Does the attentional selection bias emerge from a purely hierarchical mechanism (e.g. biasing from frontal to occipital regions)? Does attentional control work the same way for endogenous and exogenous signals (cf. Yantis, 2005 and Beck & Kastner, 2005)?

As already pointed out above, different investigation tools can be used to study attention. While monkey electrophysiology has proven useful in the testing of the biased competition model, it is not ideally suited to study large scale networks hypothetically involved in the control of attention. Neuroimaging human studies are more adapted for this. The fMRI studies that I described in the previous section not only focused on occipital responses to visual stimuli, but also comprised whole brain analyses. For instance, Kastner and colleagues (1999) highlighted the activation of a set of brain regions located in the frontal (FEF; middle frontal gyrus, MFG; supplementary eye field, SEF) and parietal cortex (superior parietal lobule, SPL; intraparietal sulcus, IPS, and inferior parietal lobule, IPL) during the cue-to-target period, while participants prepared to perform covert visual discrimination at the periphery (top-right quadrant). Notably, none of these regions - but the IPS - exhibited any additional increase of activity when the visual display was actually presented. This suggests that only the IPS may be involved in both preparatory attention and target selection. Moreover, unlike occipital regions, this study reported analogous levels of activity in frontal and parietal regions,

when comparing simultaneous versus sequential presentation of the stimuli (cf. "sensory suppression", above). Altogether, those results suggest that frontal and parietal areas are involved in the top-down biasing of occipital responses during attentional tasks (see also yantis2005), some of them (mainly frontal areas) showing no differential activity between preparatory attention and target selection and some other showing further activity increase during discrimination of the visual stimuli compared to expectation alone (IPS). Kastner and colleagues' (1999) study constituted one of the early works evidencing the existence of a "frontoparietal attentional network" (FPAN) in humans.

While Kastner and colleagues (1999) focused on investigating the neural bases of (preparatory) attention in the absence of visual stimulation, Corbetta and colleagues (2000) investigated the fMRI activity during the preparatory orienting of attention compared to target detection/selection at expected versus unexpected locations. To do so, they used a "Posner task" composed of two main trial phases: a cueing phase (e.g. central arrow pointing to the right or the left side of the screen) that indicates to the participant where the target is most likely to appear; and a target phase during which the target appears either at the cued location (valid trials, typically 75-80%) or on the opposite side (invalid trials, 25-20%). As in Kastner and colleagues (1999), they found an increase of activity in IPS during the cueing phase compared to baseline, which was sustained also during the target phase. In some trials, the target actually never showed up after the cueing phase (catch trials). In these trials, the IPS activity remained elevated, confirming the findings of Kastner and colleagues (1999) that IPS (plus other frontoparietal regions) is involved in preparatory attention and attentional expectations. In the target phase, Corbetta and colleagues (2000) observed activation of a ventral region of the parietal cortex, the temporo-parietal junction (TPJ), most pronounced in the right hemisphere, suggesting that this region may be specifically involved in target detection. To test whether the TPJ activation reflected target detection per se or attentional re-orienting when targets appear at an unexpected location (invalid trials), they directly compared invalid and valid trials. This highlighted again activation of the right TPJ, suggesting its role in the re-orienting of spatial attention.

Together with Kastner and colleagues (1999), Moore & Armstrong (2003) and the model proposed by Chelazzi and colleagues (1998), Corbetta and colleagues' (2000) study highlights the role of specific brain structures in a set of processes leading to an efficient attentional control. These brain structures contribute to the control of attention on the basis of information coming from previous experience (e.g. expectations) and from pop-out sensory features. Some of these structures may integrate the relevant information in order to perform the most adaptive attentional orienting behavior (e.g. IPS both in Kastner, Pinsk, *et al.*, 1999 and Corbetta, Kincade, *et al.*, 2000 and FEF in Moore & Armstrong, 2003) and some others may be involved in the dynamics of attentional

orienting (e.g. TPJ). On the basis of these findings, Corbetta & Shulman (2002) proposed a new model of attentional control that has been - and still is - very influential. They constructed their model on the traditional distinction between endogenous and exogenous attention, respectively referred to as "top-down" and "stimulus-driven" control of attention, in their terms. In fact, rather than considering a single attentional network, they described two networks with distinct but collaborative roles (cf. also Vossel, Geng, *et al.*, 2014). In that model, the role of the so-called "dorsal FPAN" (mainly including the IPS, the SPL and the FEF; figure 1.5A) is twofold. First, it is involved in the construction and the maintaining of the "attentional set" (e.g. the target template) during preparatory attention (cf. Kastner, Pinsk, *et al.*, 1999, and model of attentional control in Chelazzi, Duncan, *et al.*, 1998). This hypothetical function is supported by studies reviewed in Corbetta & Shulman (2002) showing overlaps between attentional and working memory task (cf. also the discussion section in Chelazzi, Duncan, *et al.*, 1998, see also above). Second, areas of the dorsal FPAN are involved in stimulus/action selection (e.g. target selection, eye movements, see Tehovnik *et al.*, 2000, cited by Moore & Armstrong, 2003). The "ventral FPAN" (figure 1.5A and 1.5B) is mostly lateralized in the right hemisphere and includes the TPJ, plus ventral frontal regions such as the inferior frontal gyrus (IFG). Its role is less understood and still highly debated (Downar *et al.*, 2002; Indovina & Macaluso, 2007; Doricchi *et al.*, 2010; DiQuattro & Geng, 2011; DiQuattro, Sawaki, *et al.*, 2014).

The ventral FPAN has been hypothesized to provide some dynamic modulation of the top-down control activity, in particular in the presence of unattended/unexpected but behaviorally relevant stimuli. In Corbetta and colleagues (2000), the TPJ was more active on invalid than on valid trials, but still it was also activated during the target phase in the valid trials. Similarly, Corbetta & Schulman (2002) reviewed studies showing higher activations in the ventral FPAN during the selection of low-compared to high-frequency stimuli at expected locations. Thus, it is not clear whether the ventral FPAN is involved in spatial attentional shifts (e.g. in an invalid trial context, such as invalid trials in the Posner paradigm) or more generally in the detection of unexpected events (e.g. in the presence of low-frequency stimuli). Either ways, the "circuit-breaking" function of the ventral FPAN is plausible if one considers both attentional shifts and unexpected stimuli selection at an attended location, as consequences of changes in the attentional set. This interpretation constitutes the basis of the model of visual attention in Corbetta & Schulman (2002): occipital areas send information to both the ventral and dorsal FPANs components (bottom-up control) while the dorsal FPAN biases occipital areas responses (top-down control) (cf. Kastner, Pinsk, *et al.*, 1999; Corbetta, Kincade, *et al.*, 2000; Moore & Armstrong, 2003). The top-down control arising from the dorsal FPAN is maintained in cases where the actual visual configuration fits the current expectations/attentional set. However, the ventral FPAN estimates the behavioral relevance of unexpected and/or

unattended stimuli (e.g. "an alarm rings in a museum", in Corbetta & Shulman, 2002), or novelty (e.g. low-frequency targets) and breaks the current top-down control. Note that the model does not include any direct feedback from the ventral FPAN to occipital areas, but rather an indirect effect of the ventral FPAN via the dorsal system (figure 1.5B). In sum, this model provides us with some insight on the various computations taking place during visual attentional control: it involves multiple functionally specific frontal and parietal regions that interact with each other in order to bias activity in the occipital cortex on the basis of expectations, goals and stimulus salience.

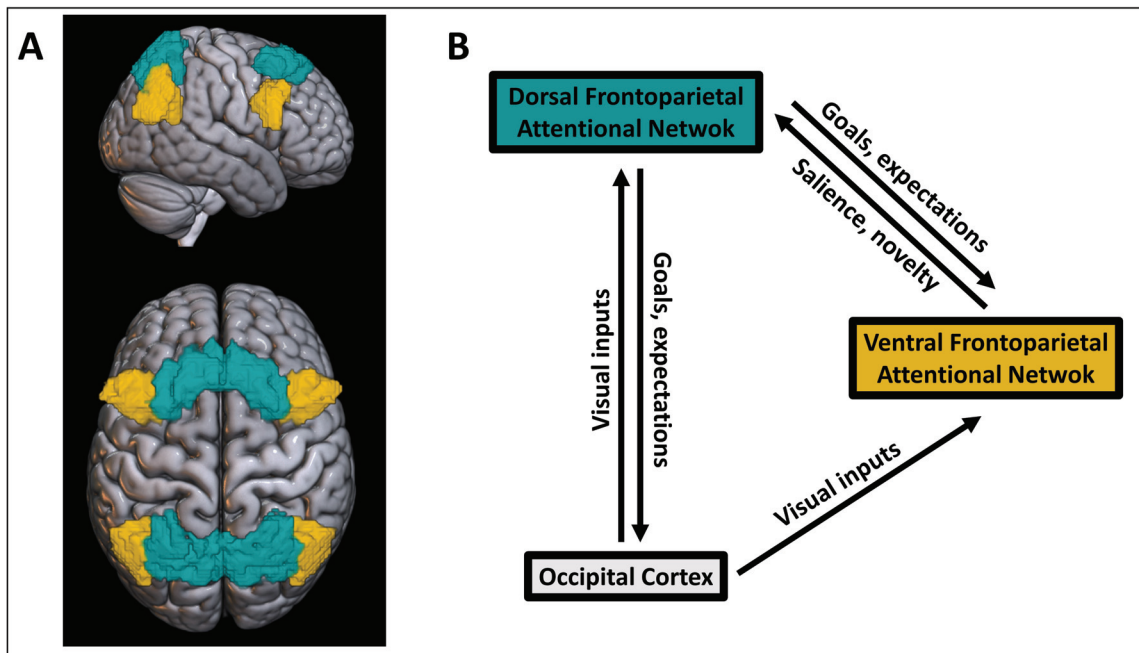


Figure 1.5: **The frontoparietal attentional networks, their hypothetical roles, their functional relationship to each other and to the occipital cortex.**

A - The frontoparietal network including the dorsal (IPS, SPL in Brodmann area 7 and FEF in Brodmann area 8; blue) and the ventral (TPJ in Brodmann area 39 and IFG in Brodmann area 44; yellow) FPAN. **B** - Adaptation of the model from Corbetta & Schulman (2002). The dorsal FPAN exerts top-down control on both the occipital cortex and the ventral FPAN so that the occipital representation of task-relevant visual items/portions of the space is boosted during visual attentional tasks. The ventral FPAN takes into account the visual information and detects the presence of unexpected stimuli. It consequently biases the top-down control of the dorsal FPAN, hence its role of "circuit-breaker". Importantly, the model does not include direct ventral FPAN - occipital connectivity.

The Corbetta & Schulman's (2002) model has been the starting point of an extensive debate regarding the role of the ventral FPAN and its relation to the dorsal FPAN. The most critical aspect in Corbetta & Schulman (2002) lies in the "type" of attention triggering responses in the ventral FPAN, and how this network can contribute to biasing occipital responses. Corbetta & Schulman (2002) state "this [ventral] network might represent the exogenous orienting system, which directs attention to the spatial locations of salient stimuli", although they also emphasize the interacting nature of

the two FPANs. As discussed in the first section of this introduction (see also figure 1.2), endogenous and exogenous attentional types are often viewed as being mutually exclusive, leading to a strong dichotomy. Later studies aimed to test the robustness of the dichotomous account proposed by Corbetta & Schulman (2002). In an fMRI study, Downar and colleagues (2002) studied the link between ventral FPAN (plus other regions) and stimulus novelty, while participants passively watched a series of identical visual items that were occasionally interleaved with novel items. Novel items activated the TPJ and IFG (plus anterior cingulate cortex), but not in the dorsal FPANs, suggesting that the ventral FPAN serves to identify novel ("salient") stimuli, consistent with the model in Corbetta & Schulman (2002). However, at variance with Corbetta & Schulman's (2002) model, this study also indicated that current task-relevance is not required for the recruitment of the ventral FPAN.

Beside the specific behavioral/task-related constraints required to engage the ventral FPAN, a key feature of Corbetta & Schulman (2002) concerns the functional interactions ought to take place between the dorsal and ventral attention control systems. These have been studied using dynamic causal modeling, a method allowing the estimation of causal interactions between brain regions during a task and their modulation by experimental factors (DCM; see section "Methodological insights"). Vossel and colleagues (2012) highlighted the role of both dorsal and ventral FPANs in attentional control during a Posner task. Briefly, they first designed a set of effective connectivity models to explain the modulatory effects of leftward versus rightward attentional orienting during the task on the dorsal FPAN and the occipital cortex. The winning (best) model included an increased excitatory connectivity between the right IPS and the right occipital cortex during leftward orienting compared to rightward orienting, consistent with a top-down modulation of occipital areas coming from the dorsal FPAN. Using a second set of DCM models, Vossel and colleagues (2012) investigated the effect of cueing validity on the bottom-up connectivity occurring between the occipital cortex and both dorsal and ventral FPANs. Here, the winning model included the modulation of connectivity from the occipital cortex to the right TPJ, and from the right TPJ to the right IFG and the right IPS, with all connections being more excitatory during invalid than during valid trials. This suggests that the sensory information of "invalidity" coming from the occipital cortex (i.e. "the target is not where it was expected") is not directly sent to the dorsal FPAN, and rather it first engages the ventral FPAN that then modulates the dorsal FPAN's activity. Together, these results shed light on the "temporal sequence" of connectivity patterns that govern the interactions between the occipital cortex and the two FPANs during attentional control (see Chica, Bartolomeo & Valero-Cabre, 2011).

A related DCM study by DiQuattro and colleagues (2014) tested the hypothesis that the right TPJ act as a "circuit-breaker" (cf. Corbetta & Shulman, 2002). In this study, the participants' task was to indicate the presence or absence of a target in a

two-item visual display (one item on each side of the screen) defined by the conjunction of a spatial location (left or right) and of a color that was known in advance by the participants (e.g. an orange circle located in the left of the screen would be a target). This resulted in three possible experimental conditions: 1) no item is of the relevant color: neutral trials, 2) one item is of the relevant color but is not at the correct location: target-colored distractor trial or 3) one item is of the relevant color and is at the correct location: target present trial. DiQuattro and colleagues (2014) defined a set of models comprising only the right FEF and the right TPJ regions. The models differed in the location of the driving inputs, that is where (in FEF or in TPJ, or both) the visual inputs from the attentional task were mostly likely to "go" first, and in the modulatory effects of the different experimental conditions on the directed connectivity between the two brain regions. The model selection showed that driving inputs were mostly likely to activate both the right FEF and right TPJ. However, the FEF driving input was excitatory while it was weakly inhibitory in TPJ, both for target-present or target-colored distractor trials. The only significant modulatory effect on connectivity was the effect of the target-colored distractor trials that decreased the connectivity from FEF to TPJ. DiQuattro and colleagues (2014) concluded that, in that task, FEF activity had a causal influence on TPJ activity, suggesting a role of TPJ in "later" processing than early stimulus-driven "circuit-breaking" signaling. This would include processes related to the match/mismatch between the current sensory inputs and any top-down expectation (see also Doricchi *et al.*, 2010; Vossel, Geng, *et al.*, 2014).

In sum, activation and connectivity studies highlighted, on the one hand, some functional specificity of the two FPANs and, on the other hand, extensive functional interactions between the two systems. Vossel and colleagues (2014) reviewed that the dorsal FPAN showed higher activity during orienting after predictive cues and during search tasks, while the TPJ showed on the contrary lower responses during those tasks. During orienting to exogenous cues, reorienting and response to contextual cues (e.g. see DiQuattro & Geng, 2011; Natale, C. Marzi, *et al.*, 2010), however, both FPANs showed high responses. In fact, depending on the "sensory situation", attention may require to recruit different brain areas/FPANs. Still, the dorsal FPAN activates consistently during attentional tasks (but see Won *et al.*, 2020; Geng & Duarte, 2021, next section and Discussion section), and it is acknowledged to be a major source of biasing of the occipital cortex activity (Vossel, Weidner, *et al.*, 2012; Moore & Armstrong, 2003). Importantly, the lack of differential activity in the ventral FPAN between any two experimental conditions does not imply that this network is "silent"/does not interact with the dorsal FPAN: again, depending on the task at hand, the ventral FPAN may be more or less inhibited by the dorsal FPAN (DiQuattro & Geng, 2011; DiQuattro, Sawaki, *et al.*, 2014; Vossel, Geng, *et al.*, 2014). Consistent with the idea that the dorsal FPAN can "judge" the need to recruit or not the ventral FPAN (and consequently inhibit or not) implies

that it is sensitive to various attentional contexts and that it does not just endorse the role of "biasing activity of sensory areas in a top-down manner". Accordingly, dorsal parietal areas (IPS, and posterior parietal cortex; PPC) can show larger activation in the presence of a salient item during a search task or during attentional reorienting, as shown using fMRI (Melloni *et al.*, 2012; Won *et al.*, 2020; Vossel, Geng, *et al.*, 2014), depending on the context, see also next sections. In addition, some specificities within the dorsal FPAN seem to depend on whether endogenous or exogenous signals are at play. For example, Buschman and colleagues (2007) showed, using monkey electrophysiology, that during visual search (i.e. "find a predefined target among four items, one being a salient distractor") the FEF neurons representing the target location responded before neurons in the lateral intraparietal region (LIP, considered the homologue of IPS in humans, e.g. see Vossel, Geng, *et al.*, 2014). The reverse pattern was observed during a pop-out task (i.e. "find a predefined target among four items, the target being also the salient item" (see also Ibos *et al.*, 2013, but see Bowling *et al.*, 2020 for conflicting results). Again, these results emphasize the importance of inter-regional dynamics, rather than mere local functional specificity.

In the section 1.1.2 ("Behavioral approach of attention control"), I mentioned that behavioral studies had highlighted how endogenous and exogenous attention independently contribute to modify behaviors but also, and most importantly, how they jointly contribute to it. In the section 1.3.1. ("The biased competition model"), I reviewed evidence on occipital response to both endogenous and exogenous attention. In the current section, I reviewed some of the work concerning the role of the dorsal and ventral FPANs, as a function of both endogenous and exogenous control. However, the study of the brain mechanisms underlying the joint influence of both types of attention has emerged more recently, which makes these mechanisms still poorly understood. This will be the main focus of the next section.

1.4 An integrative account of attentional control: the priority maps framework

In the ongoing debate about the functioning of the FPAN systems (e.g. Corbetta & Shulman, 2002; Doricchi *et al.*, 2010; Chica, Bartolomeo & Valero-Cabre, 2011; Chica, Bartolomeo & Lupiáñez, 2013; Vossel, Geng, *et al.*, 2014), the role of attention control in real-life conditions has been largely neglected. Of note, this may have contributed to the ambiguity regarding the specific role of the different regions composing the FPANs, in particular the first-glance dichotomy between endogenous and exogenous control supported by dorsal and ventral FPANs, respectively. Parallel to this debate, an alternative framework has emerged, where attentional control is thought as a "priority manager" (see definition of attention, in the "Cognitive psychology of attention" section,

above), where "attentional priority signals" can be thought as the inputs to "attention priority maps". Priority signals are any sensory or "internal states" that contributes to attention control, as I will discuss in detail in the next sections. In this framework, one is not specifically interested in what region/network is responsible for the processing of a particular type of signal, but rather the focus is on identifying response patterns that match the attentional gain attributed to each stimulus of the current visual input, and/or the behavioral output associated with the sensory input. The priority maps framework is, thus, a conceptual tool that allows matching specific sensory inputs/task conditions (e.g. "this salient square in the top-left corner of the screen") to specific brain responses (e.g. "the specific brain representation of the salient square in the top-left corner of the screen") and to specific behavioral outputs (e.g. "participants are faster at identifying the shape of the salient item in the top-left corner of the screen when they know in advance that it will be a square").

The priority maps framework largely relies on the definition of the attentional priority signals that, via competition, determine attentional selection and the allocation of the available processing resources. In the previous section, most of the studies focused on a single priority signal (e.g. endogenous cueing in Kastner, Pinsk, *et al.*, 1999; Corbetta & Shulman, 2002; Doricchi *et al.*, 2010; Vossel, Weidner, *et al.*, 2012; stimulus-driven salience in Downar *et al.*, 2002; Beck & Kastner, 2005; Indovina & Macaluso, 2007; set-relevance in Natale, C. Marzi, *et al.*, 2010; salience-based contextual cueing in DiQuattro & Geng, 2011), which precluded the study of attention control within the priority maps framework (i.e. the joint influence of multiple attentional signals on brain and behavioral processing, see Macaluso & Doricchi, 2013). In addition, those studies' results have mostly been interpreted in the context of the endogenous/exogenous attention (and dorsal/ventral FPN) dichotomy, often resulting in contradicting conclusions and hampering the understanding of attention as an integrative function that can take into account multiple signals for guiding behavior in real-world conditions. In fact, the priority maps framework attempts to explain how, in terms of brain computations, one attends to "that specific spatial location containing that specific item" rather than "that other location containing that other specific item".

1.4.1 Saliency maps: representations of attention-grabbing locations in the visual environment

There is a primary condition for any brain region to be a candidate priority map: to represent space. When introducing visual perception in the brain, I mentioned that there are parts of the brain that are retinotopically organized, which is a form of brain representation of the space (but not the only one, cf. for example "somatotopy"). Of course, occipital areas are retinotopically organized (Engel, 1997; Dumoulin & Wandell, 2008; Purves, 2008). The occipital retinotopy is often measured, using fMRI, by having

participants passively watching a screen containing various types of highly salient stimuli (checkerboard-like rotating wedges and expanding rings, e.g. see Tootell *et al.*, 1998), while fixating the center of the screen. These stimuli trigger the response of neurons that receive the time-to-time visual stimulation at a given spatial location on the screen (Engel, 1997; Dumoulin & Wandell, 2008). Importantly, occipital areas are not the only brain areas showing a retinotopic organization: this is also the case of IPS (Swisher *et al.*, 2007) and more generally of the areas composing the dorsal FPN (Silver & Kastner, 2009; Jerde *et al.*, 2012; Mackey *et al.*, 2017). Retinotopic mapping studies make use of stimuli with equal levels of salience and typically stimulate a single location of the visual field at a time. Thus, they can only assess the spatial organization of occipital and dorsal frontoparietal regions. Although this is a fundamental criterion for a brain region to be a priority map, this is not the only one.

A second specificity of a hypothetical priority map is its ability to code features in space. That is, a priority map "recognizes" the physical properties of items - more exactly their distinctive features compared to the rest of the visual scene (e.g. a color singleton or a high contrast region of the space) - and attributes a given gain to those physical properties as a function of spatial coordinates (Itti & Koch, 2001; Ptak, 2012). Models of stimulus-driven attention (Koch & Ullman, 1985; Itti & Koch, 2001) posit that all visual stimuli are spatially represented in a brain "saliency map" as a function of their "saliency power". In these models, attention is drawn towards the most salient item/region of the space in the hypothetical situation where the organism has no specific goal (Itti & Koch, 2001, see also data suggesting that attention or eye movements are first directed towards salient items irrespective of their task-relevance, see Geng & DiQuattro, 2010; Theeuwes, 2010). In other words, this is the differential salience between a given item/region of the space and the surrounding items/regions of the space that determines the gain values in the saliency map. The highest "gain peak" in the saliency map wins the competition between the salience-based representation of the whole visual scene in a "winner-take-all" fashion, thus determining where attention will be directed.

The saliency map framework fits well with experimental results obtained as part of the biased competition model for at least two reasons. First, the activity of occipital neurons increases as the contrast of the stimulus presented in their receptive field increases, even when voluntary/endogenous attention is not directed towards that stimulus (Reynolds & Desimone, 2003). This is in line with salience coding taking place locally within the occipital cortex (see for example figure 1.7A and 1.7B, where figure 1.7B represents the salience gains of spatial locations in figure 1.7A, mimicking the responses of a hypothetical saliency map in the brain). Second, the representation of each stimulus in the saliency map enters a competition for attentional selection via mutual inhibition (Beck & Kastner, 2005; Yantis, 2005).

Accordingly, the saliency maps framework accounts for various experimental results regarding attentional control (Reynolds & Desimone, 2003; Beck & Kastner, 2005; Yan-

tis, 2005), as well as more general principles related to the biased competition model (see Desimone & Duncan, 1995). However, its focus mainly regards the "bottom-up/exogenous/stimulus-driven" part of attentional control. From an "attentional priority signal" perspective, in fact, the emphasis of the saliency maps approach is put on the relative low-level physical properties of the stimuli. Attentional control is of course about those low-level signals, but also about the organism's internal state (e.g. see Moran & Desimone, 1985; Desimone & Duncan, 1995; Chelazzi, Duncan, *et al.*, 1998; Kastner, Pinsk, *et al.*, 1999; Corbetta, Kincade, *et al.*, 2000): hence, the "priority maps" framework.

1.4.2 Priority maps: integrated spatial representations of attentional gains

Most of the time, real-life situations imply the presence of multiple concurrent priority signals within the visual scene (Macaluso & Doricchi, 2013). The saliency maps framework (Koch & Ullman, 1985; Itti & Koch, 2001) emphasizes the interactions/competition between low-level external signals. The priority maps framework is based on a similar view, but it includes also the contribution of endogenous factors, that - together with low-level external signals - participate in the attribution of attentional gains to specific locations of the map. Accordingly, it is the integration of both endogenous and exogenous factors that finally determines the attended location, via a winner-takes-all mechanism (figure 1.6). The principles and functioning of the priority maps have mostly been described at theoretical and modeling levels (Koch & Ullman, 1985; Itti & Koch, 2001; Thompson & Bichot, 2005; Gottlieb, 2007; Ptak, 2012; Zelinsky & Bisley, 2015; de Groot *et al.*, 2016; Todd & Manaligod, 2018; Bisley & Mirpour, 2019).

Thompson & Bichot (2005) and Gottlieb (2007) reasoned that regions of the dorsal FPN are good candidates to endorse priority maps functions, because their activity is related to attentional control (e.g. see Kastner, Pinsk, *et al.*, 1999; Corbetta & Shulman, 2002) and they represent the visual space (Swisher *et al.*, 2007), specifically when the participants have an attentional- or memory-related task to perform (Silver & Kastner, 2009; Jerde *et al.*, 2012; Mackey *et al.*, 2017). On that basis, Thompson & Bichot (2005) reviewed experimental evidence in support of the saliency/priority maps models. The reviewed experiments were mostly monkey electrophysiology studies where the activity of FEF neurons responsive to the target and of FEF neurons responsive to the distractor(s) was recorded simultaneously. These studies showed that during a visual search task, the activity of neurons representing the target was higher than the activity of neurons representing distractors. In addition, when one distractor was salient compared to the other distractors, the activity of the corresponding FEF neurons was larger than the activity of FEF neurons representing non-salient distractors (Thompson & Bichot, 2005). These modulations appear to nicely reflect the gains expected within a priority map. Related findings have been obtained also in the LIP (Bisley & Mirpour, 2019).

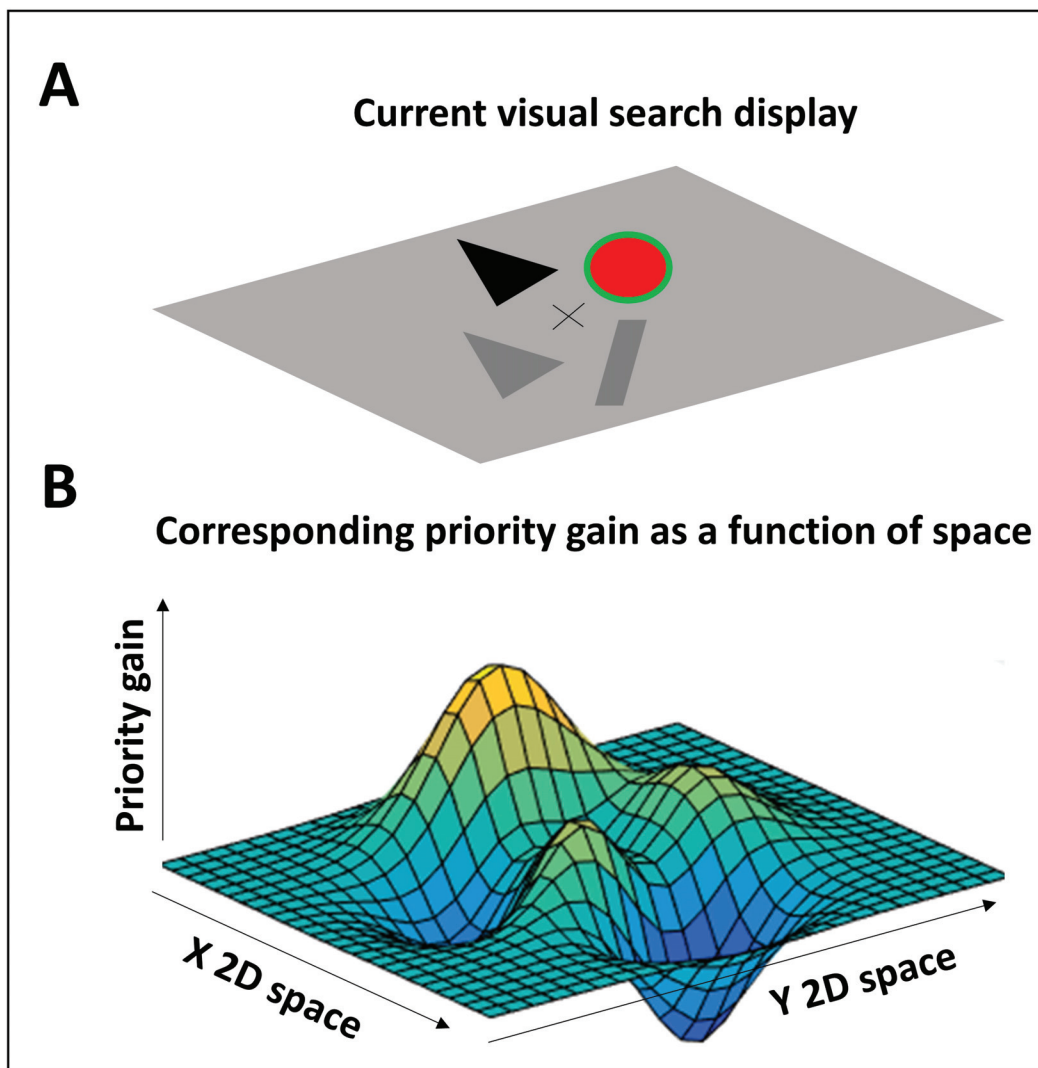


Figure 1.6: Illustration of a spatial priority map during a search task (adapted from Chelazzi, Estocinova, *et al.*, 2014).

A - Example of search array, where the participant's goal is to find the black triangle among 3 distractors. The grey triangle is task-relevant and non-salient. The grey bar is task-irrelevant and non-salient. The red and green circle is task-irrelevant and salient. **B** - Priority gains (brain responses) as a function of the 2D space. Here priority gains are attributed according to the task-relevance and the salience of the stimuli: highest priority gain peak is for the black triangle representation (target), intermediate peaks are for the salient task-irrelevant salient circle representation and the non-salient task-relevant grey triangle representation and the lowest peak is for the non-salient task-irrelevant grey bar representation.

Ptak (2012) reviewed additional evidence about the functional properties of neurons of the FPN in monkey (LIP neurons, in particular). Importantly, Ptak (2012) underlined the fact that neurons' activity in a priority map should code information in a feature-independent manner, for example: they should code salience in the same way for contrast-salient and color-salient stimuli (see also Itti & Koch, 2001). Most of the LIP monkey neurons are unselective for specific visual features (e.g. the color), consistent with the feature-independence coding principle of the priority maps framework (Ptak,

2012). However, top-down bias can counteract this principle. For example, when color is the relevant task dimension, then the LIP neurons can transiently become selective to color (Ptak, 2012). This, again, is consistent with the integration of both endogenous and exogenous factors in a putative priority map.

While these studies indicate a possible role of the dorsal FPAN in the representation of attention priorities, the main scope of the priority framework concerns providing an account for the integration of different types of attention control signals. As extensively discussed in the sections above, this has traditionally concerned the role of goal-related endogenous signals and stimulus-driven exogenous signals (Corbetta & Shulman, 2002; Buschman & Miller, 2007; Chica, Bartolomeo & Valero-Cabre, 2011; Ibos *et al.*, 2013; Bowling *et al.*, 2020). Nevertheless, several concerns have been raised regarding this simple endogenous/exogenous dichotomy. Indeed, Awh and colleagues (2012) described forms of priority signals which could neither be viewed as endogenous nor as exogenous. In particular, the authors focused on two signal-types breaking the traditional boundary between endogenous and exogenous signaling. These concerned the role of "selection history" and "reward" (albeit, it should be noted that other forms of priority signals have also been considered: e.g. "emotional salience" in Vuilleumier, 2005; Todd & Manaligod, 2018 or "social factors" in Klein *et al.*, 2009). The next sections will review the contribution of statistical learning and reward to attentional control.

1.4.3 Statistical Learning

Statistical learning refers to the attentional biasing towards particular items, or regions of the space, on the basis of their learned/known statistical regularities (e.g. their probability of occurrence). A simple case of attentional control being biased by learning-related is the comparison of behavioral abilities to find a target among distractors when the target-defining feature changes across trials (e.g. sometimes the target is red, sometimes it is vertical) versus when it does not change across trials (e.g. "pure experimental blocks" of red targets). Participants are better at performing in the second case than in the first one. The critical difference between endogenous, goal-directed attention and selection history is that selection does not bias attention towards the goal itself, but towards items/locations there are most likely to be/contain the goal (see Awh *et al.*, 2012). Ferrante and colleagues (2018) directly tested the behavioral effect of "trial history" on the attentional bias towards specific regions of the space, as well as its interaction with stimulus-driven salience. To do so, they focused on the implicitly learned probability of occurrence of different items (i.e. the target or singleton salient distractors) presented in particular regions of the screen ("statistical learning"). The participants performed a visual search task to find the target item among three distractors. In a series of four experiments, Ferrante and colleagues (2018) varied two factors: 1) the display configuration (either all stimuli were of the same color, HD, see above; or one of the three distractors was

a color singleton, SDD); and 2) the probability for the target and the salient singleton distractor to appear in a given screen quadrant. In the first experiment, the target had high probability to appear in one quadrant (high target probability location; HTPL), low probability to appear in another quadrant (low target probability location; LTPL), and an intermediate probability to appear in the two remaining locations (intermediate target probability locations; ITPL). In this first experiment, the salient distractor was equally likely to appear in each of the four screen quadrants. They found that behavioral performance increased as the probability of the target location increased (target at HTPL > target at ITPL > target at LTPL). In addition, performance was poorer when the trial included a distractor singleton (SDD) than when the stimulus array was homogenous (HD). Lastly, this difference was larger on trials when the salient distractor appeared at HTPL. Thus, the attentional priority was implicitly given to the HTPL, which was advantageous when the target appeared there.

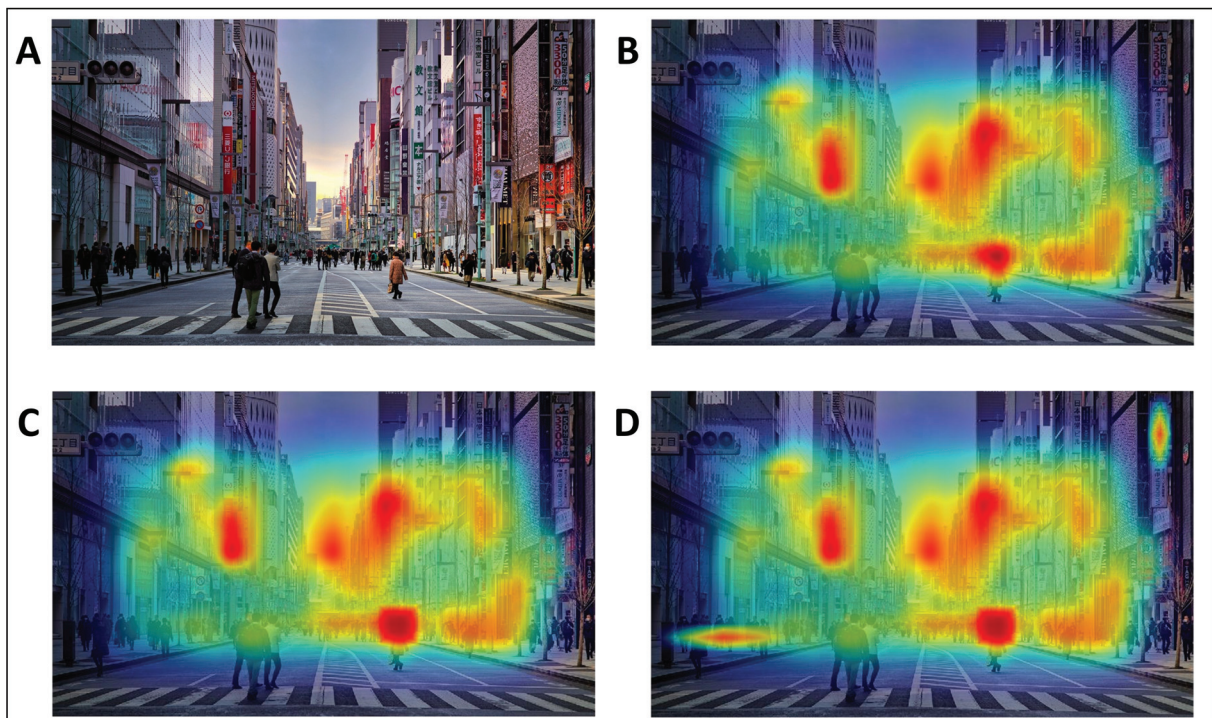


Figure 1.7: **Attentional priority gain in naturalistic visual stimuli, as a function of the types of signal taken into account.**

A - A naturalistic visual scene. **B** - The saliency map of the visual scene computed using the Graph-Based Visual Saliency (GBVS; Harel and colleagues in Schölkopf *et al.*, 2007, <http://www.vision.caltech.edu/>). **C** - Priority map of the visual scene taking into account the bottom-up salience of visual stimuli, plus the current goal of the observer: e.g. "find my friend, who is wearing a beige coat". The same GBVS computation as in B was used, but the gain around the woman wearing the beige coat has been enhanced. **D** - Priority map of the visual space, this time taking into account visual salience, the current goal (same as in C), plus statistical learning (e.g. "my friend often waits for me on the left sidewalk of this street"; gain enhanced at the bottom-left sidewalk location) and motivation ("this is my favorite chocolate shop!"; gain of the priority map enhanced at the top-right signboard location).

The follow-up experiments used the same visual displays/task and tested the effects

of changing the probability of salient distractor location, and changing the probability of both target and salient distractor location. The conclusions were similar and coherent for target and distractor location probability unbalances: 1) a target appearing at the HTPL facilitates the visual search; 2) a salient distractor appearing at HTPL reduces the search performance; 3) a salient distractor appearing at an "high-probability distractor location" produces a weaker interference on the target search compared to when the distractor appears at "low-probability distractor location". Hence, spatial selection history biases both target selection and distractor filtering/suppression processes.

In terms of brain mechanisms, statistical regularities have been mostly studied in the context of attentional reorienting (see previous section) by manipulating the (un)certainly of the cueing information, which has typically led to the growing literature on the role of both the ventral and the dorsal FPAN in the reorienting of attentional priorities (Doricchi *et al.*, 2010; Vossel, Weidner, *et al.*, 2012; Vossel, Geng, *et al.*, 2014; Vossel, Mathys, *et al.*, 2015). The literature on distractor suppression has also highlighted the involvement of regions of the FPANs in suppressive mechanisms (Melloni *et al.*, 2012; Chelazzi, Marini, *et al.*, 2019; Won *et al.*, 2020), thus underlining the roles of those brain areas beyond the classical endogenous/exogenous dichotomy of attentional control. The main issue here is that the priority maps framework calls for experimental support focusing on (the modulation of) the spatial representations of the stimuli, as a function of the statistical regularities of target/distractor location or presence (cf. also section 1.4.5 below, on the effect of statistical learning in the occipital visual cortex).

1.4.4 Reward

A second form of priority signal that goes beyond the traditional dichotomy between endogenous and exogenous attention concerns the effect of reward/motivation. Here, reward and motivation are tightly linked because reward (i.e. the fact of receiving something pleasant after a given event) triggers motivation, if it is always/often associated to the same event (Chelazzi, Perlato, *et al.*, 2013; Chelazzi, Estocinova, *et al.*, 2014). Thus, it is a particular form of trial history, but it involves reward rather than the learned regularities concerning the presence/absence of a given item in visual display or a specific spatial location. In the past few years, there has been multiple theoretical accounts linking reward to attentional control (Pessoa, 2010; Anderson, 2016; Chelazzi, Perlato, *et al.*, 2013), but the experimental work as part of the priority maps framework has not been fully developed yet (Anderson, Laurent, *et al.*, 2011; Buschsulte *et al.*, 2014; Chelazzi, Estocinova, *et al.*, 2014). For example, as a form of trial history, does motivation lead to similar effects as statistical learning on occipital and/or frontoparietal activity? The main particularity of motivation is that it can be fully dissociated from goal-directed attention, which may not be true for statistical learning that instead always concerns the location/presence of targets or distractors. For instance, Anderson and colleagues (2011)

had participants performing a visual search task. In a training phase, on each trial, participants had to indicate the (vertical/horizontal) orientation of the target bar among five non-target items. The target was defined by the color of the circle that encircled it (green or red). The participants received a monetary reward when they correctly responded to the targets: reward was high for one of the two target colors (e.g. green) and low for the other (e.g. red). All non-targets were also encircled by a colored circle, that was never green or red. In that way, participants associated a circle color with higher reward. The monetary gain was fully irrelevant for the task at hand. In the test phase of the experiment, the target was made more easily distinguishable from the non-target, it was now embedded in a colored diamond (that was never of the "high reward" color), while non-targets were still encircled by a colored circle. The task was unchanged, but now no reward was delivered. On half of the trials, one of the circle encircling the non-targets was of the high reward color. The target-search performance was slower on those trials than when the high reward color was absent in the display, suggesting that reward-associated stimuli bias attentional control even though they are fully task-irrelevant and no more associated with reward.

Chelazzi and colleagues (2014) reported a similar effect, but this time associating high, intermediate or low reward to specific spatial locations within a 8-item stimulus display. After a training phase when participants associated specific reward probabilities to specific target locations, the test phase included displays comprising, this time, two targets. For the analysis, Chelazzi and colleagues (2014) focused on the trials when participants were only able to correctly report one of the two targets. Their hypothesis was that, in these conditions, the participants would report the target located in the quadrant that had been previously associated with high rewards during the training phase. The results confirmed their predictions, highlighting that reward can bias attentional priorities towards specific spatial locations.

At the brain level, reward-based signals include the modulatory effect of occipital and dorsal FPN regions by dopaminergic signals (Anderson, Kuwabara, *et al.*, 2017) coming from the basal ganglia (Anderson, 2016). As for endogenous, exogenous and learning-based attention, nodes of the dorsal FPN are involved in the control of attention in the presence of reward signals. In a human fMRI study, Bourgeois and colleagues (2022) designed a search task where participants had to discriminate the orientation of a target bar circled in a colored circle among seven colored distractor circles. In an association phase, the circle containing the target bar could only be of two possible colors: a high reward color (e.g. green, associated with a high monetary gain for a right discrimination of the target bar) or a low reward color (e.g. red, associated with a low monetary gain for a right discrimination of the target bar) (cf. Anderson, Laurent, *et al.*, 2011, and see above). During the subsequent test phase, the color of the circle containing the target bar was never the high or the low reward color. However, on 50% trials, one of the

seven distractor circles was of the high or low reward color (25% each), while on the 50% remaining trials all distractor circles were of a color that had never been associated with reward. Bourgeois and colleagues (2022) found that the presence of a distractor circle that had been associated with reward in the association phase induced higher FEF responses (especially for distractors associated with high reward) than displays containing only distractors non-associated with reward. Correspondingly, distractors previously associated with reward lead to poorer behavioral performance than neutral distractors. These results suggest that stimuli associated with reward receive higher attentional priority and recruit regions of the dorsal FPAN (here the FEF), even when the stimuli are no more associated with reward (cf. also behavioral results reported above).

These results highlight the roles of the dorsal FPAN in shaping attentional priorities, beyond goal-directed and stimulus-driven signals, but as for the case of selection history/statistical learning, they did not specifically assess spatially-specific modulation of putative priority maps, especially in the presence of multiple priority signals. An important feature in the priority maps framework is that, in fact, priority maps may not be observable only in regions of the FPANs, but may rather occur at different stages of the visual processing pathway (Melloni *et al.*, 2012; Ptak, 2012). Accordingly, in the next section, I will review studies focusing on the influence of spatial attentional priorities in the occipital cortex.

1.4.5 Spatial priorities in the occipital cortex

It is well emphasized that activity of the FPANs bias the activity of the visual cortex (Ptak, 2012; Vossel, Weidner, *et al.*, 2012; Vossel, Geng, *et al.*, 2014). Still, one might argue that occipital areas cannot be fully considered as priority maps because their activity is mostly driven by bottom-up signals (Itti & Koch, 2001; Bisley & Mirpour, 2019). This is certainly true when visual information first enters the occipital cortex (e.g. see Theeuwes, 2010, for a temporal account of attention control), and in the absence of any expectation (see Kastner, Pinsk, *et al.*, 1999, for evidence about occipital activity related to expectations even with no visual stimulation). Further, endogenous goal-directed attention is known to modulate visual responses in the occipital cortex (e.g. see the seminal work of Heinze *et al.*, 1994). In fact, the study of priority map-like response in the occipital cortex may even be easier than in the dorsal FPAN regions. The advantage of the focus on the occipital cortex is twofold. First, spatial responses in the occipital cortex can be easily and reliably determined (Engel, 1997; Dumoulin & Wandell, 2008; Melloni *et al.*, 2012) for example using a simple spatial localizer task (Melloni *et al.*, 2012), compared to regions of the dorsal FPAN that require more complex fMRI scanning protocols and analysis methods (e.g. Swisher *et al.*, 2007; Silver & Kastner, 2009; Jerde *et al.*, 2012; Mackey *et al.*, 2017). Second, the hierarchical organization of visual processing in the occipital cortex is well understood (see figure 1.3; Ramachandran, 2002; Yantis, 2005), facilitating

the formulation of hypotheses about the contribution of feed-forward/feedback signaling for the setting of priority maps there. Thus, the coding of priority and the relative gains of the multiple priority signals may be computed in different ways depending on the stage of processing/brain region.

Feedforward and feedback signalling during visual attention

The occipital cortex represents the external visual scene (Ramachandran, 2002, see previous section "Functional organization of the visual system"). This means that at the end of the visual processing, more or less salient items/regions of the space are reliably represented in higher-order areas of the visual hierarchy (see also previous subsection "Saliency maps: representations of attention-grabbing locations in the visual environment"). Moreover, multiple sources of different nature (expectations, statistical learning, reward, etc) contribute to bias these representations. This raises the question of how/at which stage(s) of the visual processing attentional signals are integrated (Theeuwes, 2018). Current proposals regarding the time course of attentional processes posit that, in the first place, priorities are attributed to physically salient items and that goal-related signals enter the competition in a second step of the visual processing (Theeuwes, 2010; Theeuwes, 2018). In this perspective, the first step of attentional gating occurs in a purely feedforward manner ("unbiased" representation of the visual scene). However, it should be noted that this view tends to generate some confusion, because it strongly associates the terms "feedforward", "exogenous", "bottom-up" or "stimulus-driven". In turn, this promotes the idea that occipital areas merely represent "saliency maps", rather than integrated "priority maps" (see Bisley & Mirpour, 2019). By contrast, it is pivotal here to consider that the level of processing within the visual hierarchy - as well as the type (feedforward/feedback) of signaling - may play different roles in the formation of priority maps that integrate multiple attention-related signals.

First, it is well acknowledged that goal- and expectation-related signals bias the activity in the occipital cortex (Corbetta & Shulman, 2002; Vossel, Weidner, *et al.*, 2012; Vossel, Geng, *et al.*, 2014) even in the absence of any sensory input (Kastner, Pinsk, *et al.*, 1999). This indicates that goal-related signals reach the occipital areas, via feedback signaling. Analogous results have also been found for statistical learning (e.g. Melloni *et al.*, 2012; Won *et al.*, 2020; Zhang *et al.*, 2021) and reward (see e.g. Anderson, 2016), suggesting that different types of signals may be integrated already in the occipital cortex.

Second, the early feedforward processing of salience cannot be thought as a single, isolated process: feature maps may first be computed using local contrasts within a specific domain (e.g. luminance and color), and then combined to create saliency maps that integrate attention gains across multiple visual features (Itti & Koch, 2001). Such computations are likely to involve multiple levels of the visual hierarchy, as well as local interaction within feature-specific specialized occipital regions (e.g. V1/V2 and V3).

Third, the timing and directionality of priority-related processing may vary as a function of the type of signal: salience is processed relatively fast, primarily via feedforward mechanisms, while goal-related signals - that occur more slowly - involve most likely re-entrant projections from higher order areas to the occipital cortex. Learning- and reward-related signals are thought to be relatively fast (Anderson, 2016; Theeuwes, 2018), but still they appear to - at least partially - rely on the dorsal FPN regions and, possibly, on feedback signaling (Melloni *et al.*, 2012; Won *et al.*, 2020; Bourgeois, Sterpenich, *et al.*, 2022).

In addition, computations at each stage of the priority processing are expected to be reflected at other stages, for example via distractor suppression and/or target enhancement depending on the task at hand (Geng, 2014; Chelazzi, Marini, *et al.*, 2019; Geng & Duarte, 2021). In the next sections I will examine more closely how different types of attention-related signals can affect processing at the different levels of the visual hierarchy, in the occipital cortex.

Goal- and salience-related signals

To date, at least two human fMRI studies have investigated occipital priority map-like responses using concurrent manipulations of endogenous and exogenous signals. Melloni and colleagues (2012) investigated the fMRI responses in regions of interest (ROIs) that specifically responded to a single screen quadrant, as a function of which type of stimulus was present inside each of the quadrants. Participants first performed a localizer task in order to map occipital responses to each quadrant (top-left, top-right, bottom-right, bottom-left). Because Melloni and colleagues (2012) aimed at studying different priority maps profiles across the visual hierarchy, they further parceled the ROIs in four separate regions (V1, V2, V3 and the human-homologue of V4, hV4). This resulted in a total of sixteen ROIs (four quadrant representations x four occipital regions). The main task of the participants was a visual search task in which they had to find the target (a horizontal grating) among three distractors (vertical gratings). On each trial, each of the four stimuli was placed in one of the four quadrants. There were three possible trial configurations: trials when all the stimuli had the same color (homogenous displays; HD), trials when the target stimulus had a different color compared to the three distractors (salient target displays; STD) and trials when one of the three distractors had a different color from the three remaining stimuli (salient distractor displays; SDD). The display-condition was used to operationalize the exogenous signals. The quadrant location of the four stimuli was randomized across trials. In addition, depending on the experimental run, the three display-types could be either presented in a mixed manner (i.e. each trial had equal chances to be one of the three display-types) or in a blocked manner (i.e. the same display-type was presented during the entire run). This was used to operationalize the endogenous priority signals: that is, to manipulate the participants' expectation/prior-knowledge about the presence/absence of salient targets (STD) or salient distractors (SDD). This led to a two

(blocked or mixed run) x three (HD or STD or SDD condition) factorial experimental design.

The main analysis in Melloni and colleagues (2012) consisted in comparing the effect of salience as a function of mixed/blocked-run, separately in areas V1, V2, V3 and hV4. For this, they computed a "saliency index" by subtracting the activity of ROIs representing the distractor quadrants from the activity of the ROI representing the target quadrant (see also next section, and the experimental chapters). In V1, Melloni and colleagues (2012) found that the saliency index did not significantly vary as a function of the run-type (blocked or mixed), while they found this to vary as a function of the trial-type, with no interaction. They interpreted these results as evidence that exogenous signals dominate in V1. In V2, they observed the reverse pattern: that is, an effect of the run-type but not of the trial-type. This suggests that V2 activity was mostly dominated by endogenous factors. In V3, they observed no significant effect of either factor. In hV4, they observed a significant interaction between the two factors. Overall, the authors concluded that their findings support differential priority processing throughout the visual hierarchy. This in turn could reflect the fact that priority maps exist all along the visual system, but that priorities are not defined in the same way between the different processing stages.

However, it should be noted that the absence of evidence for an effect of endogenous attention in V1 may come from the analysis strategy of Melloni and colleagues (2012). In fact, for all six experimental conditions, and in all occipital regions, they observed a positive saliency index. This signifies that the response strength of the ROI representing the target quadrant was always superior to the mean response strength of the ROIs representing the three distractors. This would correspond to the prioritization of the current goal, as represented in a priority map (see figure 1.7C). Even though the target stimulus was also defined by exogenous features (it was in fact an orientation singleton: horizontal grating compared to the three vertical gratings distractors), this "exogenous component" should have been counterbalanced by the presence of the color distractor singleton in the SDD condition, thus leading to a null saliency index value, which was not the case in Melloni and colleagues (2012). This confirms that, in this study, there was a reliable target-selection effect in all visual areas.

The second fMRI study that directly investigated the interplay between endogenous attention and salience in the occipital cortex was that of Sprague and colleagues (2018). The study was similar to Melloni and colleagues (2012), but using a slightly different methodology. As Melloni and colleagues (2012), Sprague and colleagues (2018) made use of a localizer task in order to identify spatial representations of the visual space in the occipital cortex, as well as the dorsal FPAN. In the main attentional task, two stimuli (clockwise or counterclockwise moving spirals) were presented simultaneously at different spatial locations of the visual display. On a trial-by-trial basis, the participants were cued to attend to one of two stimuli. This operationalized endogenous attention. Exogenous

attention was operationalized by parametrically manipulating the contrast (20, 40 or 80% contrast) of each of the two stimuli. There was a total of 9 combinations of the stimuli (3 contrast-levels of the attended stimulus x 3 contrast-levels of the unattended stimulus). The analyses of the fMRI data showed increased activity with increasing contrast-level, both for the attended and unattended stimulus, in the corresponding spatial representations in the occipital cortex. The same occipital regions, plus areas of the dorsal FPAN, also showed a main effect of goal-directed attention, with larger activity for attended versus unattended stimuli. Thus, both endogenous and exogenous spatial signals were found to modulate activity in the occipital cortex, but without any significant interaction.

Statistical learning in the occipital cortex

Beside the effects of endogenous and exogenous signals in the occipital cortex (see above), there is some initial evidence that also statistical learning can modulate occipital responses. Won and colleagues (2020) used fMRI to investigate distractor suppression using a similar ROI approach as in Melloni and colleagues (2012) and Sprague and colleagues (2018), but now manipulating the probability of occurrence of a singleton distractor. The task involved again searching for a target in a 4-item search display. At the beginning of each run, participants were told how probable (high or low probability) the presence of a color singleton distractor would be. Behaviorally, Won and colleagues (2020) found that the presence of the salient distractor interfered less in the high- than in the low-probability runs, suggesting that prior-knowledge about the occurrence of a salient distractor could trigger more efficient suppression/filtering mechanisms. At the brain level, they measured the quadrant-specific occipital (large ROIs comprising quadrant-specific V1-V3 responses) responses as a function of what item appeared in the corresponding quadrant (target, color singleton distractor or non-salient distractor), and of the type of run (high/low probability salient singleton distractor presence). In the low-probability condition, they found that the response of the ROI representing the salient distractor was higher than the one representing the non-salient distractors, but lower than the one representing the target location (target representation > salient distractor representation > non-salient distractors representation). However, in the high-probability condition, the response of the ROI representing the singleton was not significantly different from the response of the ROI representing the non-salient distractors. These results suggest that the knowledge concerning the probability of distraction triggers a proactive suppression process that can modulate quadrant-specific activity in the occipital cortex. This fits with the priority map account, with the reshaping the occipital priority map by reducing the weight attributed to the salient distractor representation. The whole-brain analysis of the same study revealed that the IPS (in the dorsal FPAN) responded more strongly during singleton-present trials compared to singleton-absent trials, in low probability runs. Interestingly, here, this effect in the IPS disappeared in the high probability runs. This suggests that during

proactive suppression, the filtering of highly-probable salient distractors may occur via local interactions within the occipital cortex, without the need of any further modulatory influence from the dorsal FPAN (see also Geng & Duarte, 2021).

Using a similar design, Zhang and colleagues (2021) showed that the signature of salient distractor suppression in the occipital cortex (see Won *et al.*, 2020, above) could be observed when the distractor singleton appeared at frequent spatial locations. The main difference between Zhang and colleagues (2021) and Won and colleagues (2020) is that in Won and colleagues (2020) the participants were informed about the overall probability of the occurrence of the salient distractors, but not about their location. By contrast, in Zhang and colleagues (2021) the experimental manipulation concerned the spatial location of the singleton distractor: the singleton had high probability to appear in some locations, and low probability to appear in other locations. The imaging results showed that the spatially-specific occipital activations (large V1-V4 quadrant-specific ROIs) associated with salient distractors was lower when they were presented in high probability location compared with salient distractors presented at low probability locations. This indicates the existence of spatially-specific proactive suppression within the occipital cortex. Importantly, when the target was presented in the "high singleton distractor probability location", it also produced lower activation compared to when targets appeared at other locations. This finding highlights that, rather than the distractors by themselves, expectations can modulate/suppress specific locations, and this will affect also the processing of task-relevant targets presented there (Zhang *et al.*, 2021).

Consistent with the findings of Won and colleagues (2020), also Zhang and colleagues (2021) found higher parietal activation when the singleton distractor appeared at the low probability location compared with singletons at high probability locations. Again, this is consistent with the proposal that the dorsal FPAN "disengages" when proactive suppression is effective. The occipital response patterns found in Won and colleagues (2020) and Zhang and colleagues (2021) provide us with supporting evidence for the existence of priority maps within the occipital cortex, showing that highlighting processing suppression at spatial locations learned to be detrimental for task performance.

In this perspective, one would expect that manipulating target - rather than distractor - probability (c.f. Ferrante *et al.*, 2018, above), the presentation of targets at HTPL would elicit greater occipital responses compared to targets to LTPL (see figure 1.7D) but this has not been formally tested in Won and colleagues (2020) and Zhang and colleagues (2021) (see discussion in Zhang *et al.*, 2021). However, this prediction contradicts an account positing that, actually, an "expectation suppression" effect is observable in occipital areas (Richter & de Lange, 2019; Alink & Blank, 2021). Accordingly, targets at HTPL would elicit lower occipital responses than targets at LTPL. Richter and colleagues (2019) provided fMRI evidence for this phenomenon. In a training phase, pairs of objects were presented in rapid succession (i.e. cue-object). The pairing was fixed across the

80 repetitions of each pair, so that the first object fully predicted the second object. The test phase, during fMRI scanning, also comprised the presentation of objects' pairs, but now the first object was now only 50% predictive of the second object. Moreover the participants focused goal-directed attention either to the objects (judge whether the object was "electrical" or "non-electrical") or to a streams of centrally-presented characters. The imaging results showed reduced activation of V1 for predictive versus non-predictable pairs, irrespective of attention condition. One possible explanation of this "expectation suppression" phenomenon is that the predictability of the salient distractor feature/location decreases its salience, thus leading to poorer spatial representation in priority maps (see Alink & Blank, 2021).

In sum, the study of the effects of selection history in the occipital cortex provides us with somewhat ambiguous results. On the one hand, there is evidence of spatially-specific modulation of occipital responses and - consistent with the priority framework - these appear to combine signals related to expectations, selection history and salience. On the other hand, the finding of suppressive effects for task-relevant stimuli (cf. "expectation suppression") appears in clear contradiction with the predictions of the priority framework, see also section 1.6 "Current issues and aims", below.

Reward in the occipital cortex

As noted above (section 1.4.4), behavioral evidence indicates that reward and motivation can also affect target selection, raising the question of the possible influence of reward contingencies on the activity of the occipital cortex. Using EEG, Grahek and colleagues (2021) determined the effect of reward during a feature-based attentional task. The visual display consisted in two superimposed random dot kinematograms (RDK), each of one color, flickering at different frequencies. Participants had to detect the coherent motion in the target RDK, which color was cued at the beginning of each trial. In a first phase, the behavioral responses were not associated to reward, but in a second phase one of the color was associated with high reward and the other with low reward. As the two RDK flickered at different frequencies, they elicited oscillations at different frequencies over the occipital cortex, thereby making the influence of reward on each RDK measurable using steady-state visual evoked potentials (SSVEPs). Grahek and colleagues (2021) tested the difference of SSVEPs before and during the stimulus-reward association. The results showed an increase of the SSVEPs by comparing the association phase with the pre-association (baseline) phase: the high-rewarded RDK elicited higher SSVEPs compared to baseline, both when RDK was or was not attended. This result suggests that reward can elicit increased occipital responses, comparably to goal-directed endogenous attention (Stanisor *et al.*, 2013). However, the effect of reward disappeared after the reward association phase. This suggests that reward may immediately influence occipital responses to rewarded locations, but that this immediate effect would disappear

when stimuli/spatial locations are no more rewarded (but see Chelazzi, Estocinova, *et al.*, 2014 for contrasting behavioral results).

Using magnetoencephalography (MEG), Buschsulte and colleagues (2014) investigated the effect of reward on occipital responses, specifically in the spatial domain. In this visual search experiment, there were only two stimuli in the search array, one on each side of the screen. Each stimulus contained two colors: one stimulus contained the target color plus a non-target color, while the second stimulus contained two non-target colors. The participants had to indicate where the target color was located on the "target stimulus" (right or left of this stimulus). One of the non-target colors was associated with high rewards. Hence, there were three main array configurations: 1) one stimulus contained the target color, and the other contained non-target colors not associated with high reward; 2) one stimulus contained the target color and the other contained the reward color; and 3) one stimulus contained the target and the reward color, while the other only contained non-target colors not associated with reward. Reward was only delivered in the latter case, and only when participants gave a correct response. The results showed larger MEG responses associated with the distractor stimulus when this comprised the reward color than when it did not, suggesting that reward can also bias occipital responses to distractors in addition to targets (cf. Grahek *et al.*, 2021). Importantly, this effect disappeared when the amount of reward was increased. This was interpreted as a top-down suppression of the high-reward signal which was susceptible to highly interfere with the processing of the task-relevant target stimulus/color under high-reward compared to low-reward conditions. In addition, Buschsulte and colleagues (2014) found that the passive viewing of the target color increased the activity of the visual cortex, which was not the case for the reward and the control colors. Lastly, RTs were found to be slower when the reward color was associated with the target stimulus than when it was completely absent on the search display. Together, these results suggest that feature-specific rewarded-related signals (here color) can be proactively suppressed because of their task-irrelevance.

Overall, the results concerning the influence of reward on attentional control are mitigated. While behavioral data show that reward exerts a reliable and long-lasting effect on attentional selection (Anderson, Laurent, *et al.*, 2011; Chelazzi, Estocinova, *et al.*, 2014), the results at the brain level suggest that the occipital responses related to rewarded stimuli highly depend on the task configuration (e.g. whether proactive suppression occurs or not). Importantly, the effect of reward has not been tested in the priority maps framework at the brain level (e.g. by comparing occipital ROIs spatial responses to high/low rewarded locations during attentional search tasks), as it has been more consistently done for endogenous, exogenous and statistical learning signals (cf. subsection about statistical learning, above).

In sum, the question of how priority maps are generated in the brain received growing interest in the past few years. However, it is mostly addressed using disparate protocols and theoretical backgrounds, and the resulting outcomes rarely show full coherence between theoretical accounts (e.g. the priority maps framework), behavioral and brain results (see for example the issues of "expectation suppression", proactive/reactive suppression and feedforward/feedback processing above). Hence, here I propose that the question of how attentional priorities are attributed needs to be raised via the use of standardized protocols under a unified theoretical background.

1.5 Current issues and aims

The literature presented above can be schematically split in two main fields: one regarding spatial occipital responses to attended and/or salient stimuli (e.g. Moran & Desimone, 1985; Chelazzi, Duncan, *et al.*, 1998; Reynolds & Desimone, 2003; Beck & Kastner, 2005); the other regarding the FPANs, typically disregarding stimulus location (e.g. Kastner, Pinsk, *et al.*, 1999; Corbetta, Kincade, *et al.*, 2000; Corbetta & Shulman, 2002; Indovina & Macaluso, 2007; Doricchi *et al.*, 2010; Chica, Bartolomeo & Valero-Cabre, 2011), although note that a few studies sought to connect the two (e.g. Moore & Armstrong, 2003; Thompson & Bichot, 2005; Vossel, Weidner, *et al.*, 2012; Vossel, Geng, *et al.*, 2014). Research in these two fields often made use of dedicated paradigms, making it difficult to compare results across experiments and often yielding to contradictions. The latter include the roles of the dorsal and ventral FPANs (see Chica, Bartolomeo & Valero-Cabre, 2011; Macaluso & Doricchi, 2013; Vossel, Geng, *et al.*, 2014), the endogenous/exogenous dichotomy (Awh *et al.*, 2012; Macaluso & Doricchi, 2013; Anderson, 2021), the conditions for "attentional capture" by salient stimuli (Folk *et al.*, 1992; Geng, 2014; Anderson, 2021; Geng & Duarte, 2021; Luck, Gaspelin, *et al.*, 2021) and the mechanisms underlying the attribution of attentional resources (Beck & Kastner, 2005; Vossel, Weidner, *et al.*, 2012; Vossel, Geng, *et al.*, 2014; Geng & Duarte, 2021). The development of the priority maps framework attempts to reconcile some of these contradictions and experimental gaps. In my thesis, I used the priority map framework to address 4 main issues:

First, it is well acknowledged that both task-goals and stimulus-salience can increase the local occipital representation of a stimulus (Kastner, Pinsk, *et al.*, 1999; Chelazzi, Duncan, *et al.*, 1998; Reynolds & Desimone, 2003), but how do these signals jointly affect activity in visual areas when presented at the same time? And, relatedly, how does the distribution of these signals across the visual field (i.e., same/different locations) affect the corresponding occipital visual representations?

Second, previous research has mostly focused on the study of goal- and/or salience-related signals (Melloni *et al.*, 2012; Sprague *et al.*, 2018), but other types of signals are also known to contribute to attention control (statistical learning, reward, emotions, etc; see Anderson, 2016; Ferrante *et al.*, 2018; Todd & Manaligod, 2018). This raises the question of whether these signals also modulate spatial representations in the occipital cortex. And, if so, how do these signals interact with task-goals and salience, when presented at the same time (cf. also previous paragraph).

Third, attentional signals seem to be represented differently across the visual hierarchy: some studies indicated that salience dominates spatial processing in early occipital areas, with attentional goals affecting mainly higher-order occipital areas (Itti & Koch, 2001; Melloni *et al.*, 2012; Bisley & Mirpour, 2019), but other studies challenged this

view showing that current goals can modulate activity down to the primary visual cortex (Kastner, Pinsk, *et al.*, 1999; Sprague *et al.*, 2018). These contradictions are likely to arise from the vast heterogeneity of tasks and stimuli used in the different studies. Here, I addressed this by systematically testing the influence of priority signals at different levels of the visual hierarchy, using a highly standardized experimental set-up across multiple studies (cf. Experiments 1-3 below).

Fourth, while there is a general consensus that the inter-regional connectivity between the occipital cortex and the parietal cortex is important for attention control, the specific constraints that govern these interactions remain elusive. The common view is that the dorsal FPN exerts top-down influence over the occipital cortex for goal-related control (Vossel, Weidner, *et al.*, 2012; Vossel, Geng, *et al.*, 2014), while salience-related signals would project in the opposite, bottom-up, direction from the occipital areas to the parietal cortex (Itti & Koch, 2001; Beck & Kastner, 2005; Bisley & Mirpour, 2019). However, in the presence of multiple priority signals, these inter-regional interactions do not seem to fully account for some of the experimental findings, such as target enhancement and distractor suppression (Geng, 2014; Geng & Duarte, 2021; cf. also "biased competition model", Desimone & Duncan, 1995).

In my thesis, I aimed to address these issues using a coherent experimental strategy, within the priority map framework. Specifically, I assessed how competitive interactions between multiple priority signals shape the responses of spatial maps in the occipital cortex. In a series of three fMRI studies, I tested how current goals, statistical regularities, reward and stimulus-salience jointly determine the distributed patterns of activity across the different levels of the visual hierarchy in the occipital cortex and I investigated how these signals modulate the whole-brain responses and the connectivity between these occipital regions and the dorsal FPN.

EXPERIMENT 1. The first study addressed the joint effects of task-goal and stimulus-salience on the activity of the occipital cortex. Here the experimental design crossed factorially the spatial location of the two attention priority signals, which allowed to investigate the impact of salience on target and distractor stimuli. In the priority map framework, I hypothesized that the occipital representation of the target would show greater activity than the representation of the distractors, and that salience would affect processing at both target and distractor locations. These findings would highlight the joint effects of goals and salience on the same (occipital) spatial representation of space, which may be restricted only to some of the levels of the visual hierarchy (cf. Melloni *et al.*, 2012). Further, using analyses of effective connectivity I tested the relative contribution of occipital-occipital versus occipital-parietal connectivity in determining the effects of goals and salience in the occipital cortex.

Intra-areal, occipital-occipital effects would represent competitive interactions within the priority maps, while inter-areal occipital-parietal connectivity would instead point to more distributed mechanisms of attention control (e.g. see Corbetta & Shulman, 2002).

EXPERIMENT 2. In the second experiment, I investigated the impact of statistical learning and salience on the occipital representations of space. By definition, priority maps should integrate different types of attentional gains, as a function of space. Thus, it may be expected that the repeated presentation of targets at the same location would enhance the attentional gain of their representation in the priority maps. Nonetheless, previous studies that used recurrent salient distractors at one location reported a reduction of occipital responses (cf. distractor suppression, Won *et al.*, 2020; Zhang *et al.*, 2021). Further, the same phenomenon may occur also for recurrent target locations (cf. "expectation suppression" Richter & de Lange, 2019; Alink & Blank, 2021). Accordingly, here my objective was twofold: first, to test how statistical regularities modulate the representation of target in the occipital cortex; and second, to test whether statistical learning and salience interact in the occipital representations. I made predictions according to two distinct scenarios. Concerning the first objective, if statistical learning operates via top-down control, I expected larger activity for targets presented at high-probability locations (HTPL), compared with targets presented at low probability locations (LTPL), and this may occur throughout the visual hierarchy (see Kastner, Pinsk, *et al.*, 1999; Sprague *et al.*, 2018). By contrast, if learning occurs via bottom-up mechanisms, target-related activity should be larger in LTPL compared with HTPL ("expectation suppression", Theeuwes, 2018; Alink & Blank, 2021), and may be observed in early visual cortex only (Richter & de Lange, 2019). The two scenarios would be also associated with different patterns of connectivity and different levels of interaction between statistical learning and salience. The implementation of statistical learning via top-down mechanisms leads to the prediction of increased parietal-to-occipital connectivity in the HTPL condition, with a pattern of interactions with salience similar to that expected for Experiment 1 (joint effects within the intermediate levels of the visual hierarchy). By contrast, if statistical learning operates via expectation suppression, it may be expected that local occipital-occipital connectivity will play the pivotal role; and that the relative impact of statistical learning and salience may differ across the levels of the visual hierarchy (i.e. suppression mainly restricted to the early visual cortex, salience affecting also intermediate processing stages).

EXPERIMENT 3. The third experiment investigated the effect of reward on the occipital representations, as well as its interplay with salience. While reward is known to affect the allocation of attentional resources (Chelazzi, Perlato, *et al.*, 2013; Chelazzi, Estocinova, *et al.*, 2014; Anderson, 2016), little is known about whether/how reward information is processed in the occipital visual cortex (but see Serences, 2008; Buschschulte

et al., 2014; Grahek *et al.*, 2021). The debate about reward effects as part of the priority maps framework primarily regards the extent to which reward-related biases rely on bottom-up versus top-down mechanisms (Awh *et al.*, 2012; Theeuwes, 2018) and whether they result in facilitation or suppression (cf. conflicting results in Buschsulte *et al.*, 2014; Grahek *et al.*, 2021). In turn, this generates different predictions as to the interplay between reward- and salience-related signals. In particular, if reward signals affect visual processing primarily via suppressive mechanisms, suppressive effects (cf. Buschsulte *et al.*, 2014) and competitive interactions with salience may be expected, as opposed to activity enhancement in order to promote the selection of rewarded targets (cf. priority map framework, see also Grahek *et al.*, 2021). As for Experiment 2, I envisaged two possible scenarios: one entailing the combination of reward and salience across the visual hierarchy, plus a contribution of the posterior parietal cortex; and the other relying mainly on local competitive mechanisms, affecting primarily early stages of the visual hierarchy. However, of note, suppressive mechanisms in statistical learning and reward may be different, entailing sensory versus proactive processes, thus resulting in different patterns of activation between Experiment 2 and 3 (Won *et al.*, 2020; Geng & Duarte, 2021).

In sum, in a series of three fMRI studies, I tested the main hypothesis that the occipital cortex contains representations of attention processing priorities. In the priority map framework, I assessed the spatially-specific activity when multiple attention-related signals (salience, goals, statistical regularities and/or reward) are presented simultaneously in the visual field. The main prediction was that the different signals would jointly influence occipital spatial representations. I tested this prediction at different levels of the visual processing hierarchy, considering separately activity in BA17 (V1, primary visual cortex), BA18 (V2) and BA19 that includes several specialized visual areas (V3/hV4). In addition, I used analyses of inter-regional connectivity and whole-brain activations to characterize the mechanisms that shape priority representations in the occipital cortex. In particular, I put to the test hypotheses emphasizing selection via competitive mechanisms taking place within the topographic occipital maps versus mechanisms entailing top-down/bottom-up signaling between the occipital representations and the posterior parietal cortex in dorsal FPAN. The current work will help developing the priority map framework by specifying mechanisms and constraints that govern the selection of relevant information in conditions entailing a multitude of competing signals, as it is the case in any real-life situation.

1.6 Methodological insights: how can functional magnetic resonance imaging help within the priority maps framework?

The present thesis work falls within a broader project called MAC-Brain (“Developing a Multi-scale account of Attentional Control as the constraining interface between vision and action: A cross-species investigation of relevant neural circuits in the human and macaque Brain”; <https://www.humanbrainproject.eu/en/about/project-structure/partnering-projects/mac-brain/>). The MAC-Brain project investigates attentional control using standardized visual stimulation protocols and different methodological approaches: behavior, EEG, fMRI and monkey electrophysiology. Its final aim is to develop a unified testing of the mechanisms underlying the priority attributions to multiple stimuli during visual spatial attention. To what extent can fMRI help to achieve this goal?

fMRI is not a unique technical solution to the problems that I raised/will raise all over this manuscript: fMRI is adapted to specific investigations and its usefulness depends on how one uses it (see Duncan, 1998). However, fMRI has specific advantages related to the study of attentional control in the context of the priority maps framework. First, despite its poor temporal resolution (see below), it has a relatively good spatial resolution allowing us to study activity associated with a specific stimulus, while presenting multiple stimuli at the same time (cf. Melloni *et al.*, 2012; Sprague *et al.*, 2018; Won *et al.*, 2020; Zhang *et al.*, 2021). In addition, it has the advantage of providing a measure of the brain activity at the mesoscopic scale, thus allowing us to observe changes associated with specific experimental conditions in the entire brain. Here, I detail what are the principles of fMRI and what specific types of analyses helped me to achieve this thesis work.

1.6.1 What is measured in fMRI and how is it measured?

Brain cells, as other types of cells need oxygen and nutrients to function. The transit of this metabolic support is made through the blood that circulates into blood vessels. Accordingly, these blood vessels are distributed in the entire brain. Each time brain cells increase their activity, the local blood flow proximate to the cells also increases in order to bring oxygenated blood to this specific site. This oxygenated blood flow is of considerable magnitude compared to the actual oxygen needs of the brain cells (Poldrack *et al.*, 2011), causing a transient surplus of highly oxygenated blood at the site where brain cells require oxygen. The molecule that carries the oxygen units in the blood is the haemoglobin. Depending on whether it transports oxygen molecules or not, the haemoglobin can either be in the oxy-haemoglobin or in the deoxy-haemoglobin form, respectively. These are the molecules of interest in fMRI, because these two forms have specific magnetic properties: oxy-haemoglobin is non-magnetic, while deoxy-haemoglobin

is paramagnetic. Thus, if one applies a magnetic field, the oxy-haemoglobin will not interfere with the applied magnetic field, while the deoxy-haemoglobin will disturb it.

Performing fMRI basically consists in applying magnetic fields and measuring how much brain tissues disturb these magnetic fields. In brain regions where the brain cells do not need much oxygen, the local oxy-haemoglobin/deoxy-haemoglobin ratio is low, and the deoxy-haemoglobin disturbs the applied magnetic field: locally, the spins of the hydrogen atoms rapidly dephase from the applied magnetic field, the resulting fMRI signal is relatively poor in that condition. On the contrary, in regions where there are higher needs of oxygen, the local oxy-haemoglobin/deoxy-haemoglobin ratio is high, then the measured signal is high.

The measured signal is called the blood-oxygen-level dependent (BOLD) signal. Functionally speaking, what is of interest here is the variation of the BOLD signal across the brain as a function of the task performed by participants. To do so, the brain is parceled into voxels ("3D pixels"), each of them being associated with specific BOLD signal dynamics over the course of the experiment. In univariate analyses, one predicts the BOLD signal dynamics over time as a function of experimental conditions. Of note, this prediction is voluntarily the same for all voxels: the prediction model assumes that all voxels have stereotypical BOLD variations whenever an "experimental event" occurs (e.g. visual stimulation and/or cognitive task to perform). To build this model, one first needs the "timings" of the experiment, that is, the exact time of the experiment at which the different experiment events (in fact, experimental conditions) begin (onsets), and how long they last (durations). This information enables constructing a predictor (one for each experimental condition) that reflects the expected change of BOLD signal over time in the voxel, if this is activated by the events. From the beginning of each onset to the end of the event (end time = onset + event duration), predictor values are set to "1". When there is no event, predictor values are set to "0". Because these binary predictor values do not resemble the BOLD signal dynamics over time, they are convolved with a function, the canonical haemodynamic response function (HRF), so that it matches the BOLD signal dynamics that one would predict for each experimental condition (predictors). This prediction then is related with the actual BOLD signal (fitting of a general linear model) for each voxel, resulting in "Beta" values ("how much does the actual BOLD signal increase as the predicted signal increases?"): highest Beta values mean that the actual BOLD signal increases a lot as the predicted signal increases (this is what one commonly calls "high activation" or "high haemodynamic response").

1.6.2 Quadrant-specific responses in the occipital cortex

The main objective of this thesis project is to test a set of hypotheses about the representation of spatial selection priorities in the occipital cortex (see previous section).

The relevant tests assess how the presentation of multiple attentional signals (endogenous goals, exogenous salience, trial history and reward) jointly affect the representation of space along the visual processing hierarchy (figure 1.8A). A first step to this end is to identify spatially-specific responses at the different levels of the hierarchy. For this, all our participants underwent a localizer-scan that allowed us to define voxels responding preferentially to one of the four visual quadrants (figure 1.8B). Using anatomically defined visual regions (BA17, BA18 and BA18), these quadrant-specific responses were grouped in 12 separate ROIs, each corresponding to the visual representation of one quadrant within a given level of the visual hierarchy.

Next, across three separate experiments, we investigated how the combinations of endogenous goals and salience (Experiment 1), trial history and salience (Experiment 2), and reward and salience (Experiment 3) modified these distributed representations of space in the occipital visual cortex (figure 1.8A and C). In all three studies, the stimulus display comprised four items and the task of the participant was to identify and discriminate the target stimulus.

The localizer scan: The spatial mapping along the visual hierarchy was made using a localizer task at the beginning of the fMRI scanning session, for each participant. During the localizer, the visual display comprised a fixation dot at the center of the screen and a visual array of moving bars (a few of which were right/left tilted) in one of the four quadrants only (figure 1.8B). Participants had to report the orientation of as many tilted target bars as possible, located among multiple horizontal or vertical non-targets, while maintaining central fixation. The interest of keeping the participants' gaze at the center of the screen is that the occipital representation of the four quadrants remained constant during the localizer task, which would not be the case if participants were free to move their eyes: the occipital mapping would have been reshaped/updated for each eye movement. This allowed us to obtain quadrant-specific responses in visual areas. Of note, this localizer task was fully independent of the main attentional task/manipulation. Using an anatomical mask we defined a set four ROIs (i.e. the four quadrant representations) separately for three Brodmann areas: BA17, BA18 and BA19 (cf. previous section "Functional organization of the visual system in the brain"), which resulted in a total of twelve occipital ROIs (three BAs x four quadrants).

The three display-conditions: Common to the three experiments was the operationalization of stimulus salience. To do so, we used three display-conditions: one where no stimulus was salient (HD, cf. above and figure 1.1, leftmost panel), one where the target was salient (STD, cf. figure 1.1, central panel) and one where a distractor was salient (always the one opposite to the target, in order to reduce the final number of experimental conditions, SDD, cf. figure 1.1, rightmost panel).

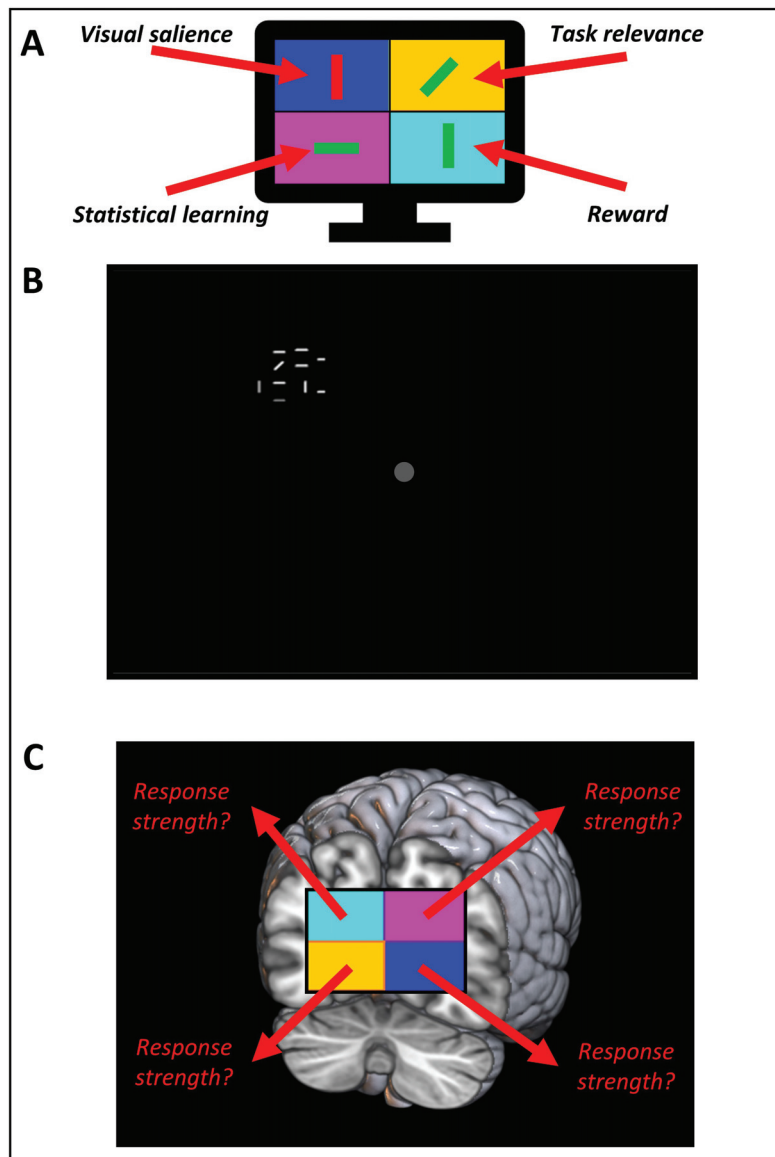


Figure 1.8: **Schematic illustration of the main experimental manipulations common to the three experiments conducted in this thesis project.**

A - On each trial, each screen quadrant was filled with a single visual item. What was manipulated is the attentional priority signal carried by each of those stimuli. **B** - Example of visual stimulation during the localizer task. An array of small moving bars appeared in each quadrant of the screen, one at a time. **C** - Illustration of the mapping between visual quadrants (cf. panel A) and the corresponding spatial representations in the occipital visual cortex.

Averaging ROIs activity as a function of target location: In each experiment, we first assessed the effect of the different types of priority signals, and their interactions (cf. e.g. HD versus STD versus SDD conditions, above), in the ROI representing the target ("ROI_IN") and the ROIs representing the opposite quadrant ("ROI_OPP"), where the salient distractor was presented in the SDD condition. Separately for each BA-region, the ROI_IN/ROI_OPP responses were computed by averaging activity of different ROIs depending on the target spatial location. Because we controlled the spatial location of the priority signals on each trial, this allowed us to track the priority gain

attributed to each priority signal at the local level of the occipital spatial representation: e.g. for Experiment 1, goal-related priority (activity of "ROI_IN" versus "ROI_OPP", irrespective of display-type), salience-related priority (e.g. activity of "ROI_IN_{STD} + ROI_OPP_{STD}" versus "ROI_IN_{STD} + ROI_OPP_{STD}"), and the corresponding interactions.

Spatial bias vectors: The data averaging described above (ROI_IN/ROI_OPP) considers only the activity of 2 out of the 4 ROIs within each BA-region. In order to obtain a more comprehensive description of spatial coding in the occipital cortex, we introduced a novel index ("spatial bias vector") that makes use of the activity in all 4 ROIs to identify any representational bias in 2D space. We describe three main steps that we followed to compute the spatial bias vectors. In the first step, for each experimental condition (see next chapters, for details), we considered the Beta values of each of the four spatial ROIs (occipital representation of the top-left quadrant, ROI_TL; of the top-right quadrant, ROI_TR; of the bottom-right quadrant, ROI_BR; and of the bottom-left quadrant, ROI_BL; see figure 1.9A-B), separately for the 3 BA-regions. As can be seen in figure 1.9B (top graph), if the top-left quadrant contained the target, the activity of ROI_TL should be higher than the activity of other ROIs, accounting for the effect of target selection. Each ROI response (figure 1.9B) was transformed into a coordinate in the 2D space as a function of the screen quadrant it represented (i.e. (-Beta, Beta) for the Beta value of ROI_TL; (Beta, Beta) for the Beta value of ROI_TR; (Beta, -Beta) for the Beta value of ROI_BR and (-Beta, -Beta) for the Beta value of ROI_BL; figure 1.9C). For each experimental condition and each BA, this resulted in four vectors (one for each ROI, figure 1.9C). This first allowed us to get a spatial representation of the activity bias taking place in each occipital BA. In a second step, for each experimental condition, we summed the four vectors in order to index the overall spatial bias within each BA-area (grey vectors in figure 1.9D). Of note, the direction of the sum-vector was the one of the quadrant-representation with the highest Beta value, typically the location of the target. This operation was repeated for each target-location, resulting in four sum-vectors (see figure 1.9D). In a third step, we collapsed the four sum-vectors into the same coordinate system, where the top-left quadrant represents the target location (figure 1.9E). This was done because our experimental designs can be seen as the repetition of the experiments across the four quadrants of the screen (i.e. the target-location is different across trials), while here we did not aim to investigate the effect of presenting the target in one specific quadrant (cf. also "averaging ROI activity as a function of target position", above). We were rather interested in understanding the effect of the different priority signals on the distributed patterns of occipital activity, irrespective of the specific top/bottom-left/right quadrant.

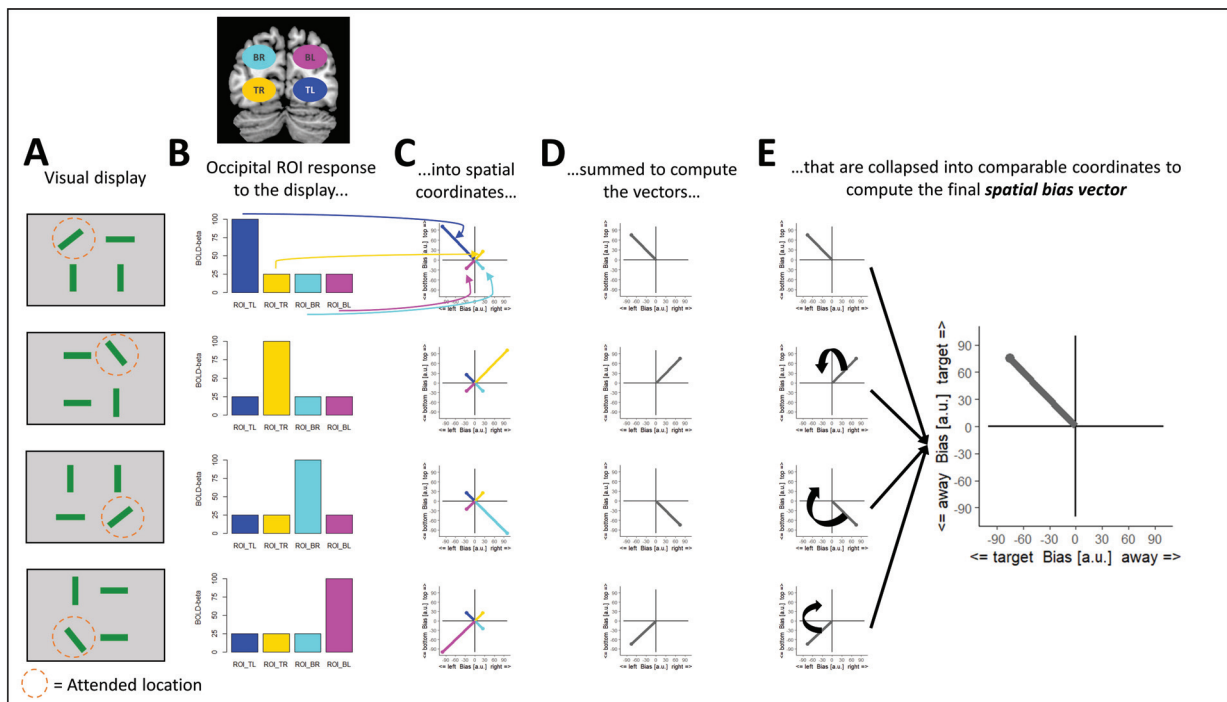


Figure 1.9: **The spatial bias vectors computation steps.**

A - Examples of visual displays, for each possible target/attended location. **B** - Example occipital ROI-activity, for each target location display. **C** - Transformation of the ROI-activity into spatial 2D coordinates (the four ROI colors vectors). **D** - The resulting sum-vector for each target location display. **E** - The four summed-vectors collapsed into comparable coordinates. TL = top-left, TR = top-right, BR = bottom-right, BL = bottom-left.

1.6.3 Brain connectivity

The project's objectives include testing hypotheses about the mechanisms underlying the priority-related modulation of the distributed representations of space in the occipital cortex (cf. above). These hypotheses concerned primarily the role of the inter-regional communication between the occipital cortex and the dorsal FPAN, which we investigated using measures of functional and effective connectivity.

We used psycho-physiological interactions (PPI; Friston, Buechel, *et al.*, 1997) as a way of assessing condition-specific changes of functional connectivity at the whole-brain level (Experiment 2). The term PPI reflects the contribution of a "seed" brain region's activity to explain other region's activity as a function of the experimental condition. Thus, the principle of PPI is based on the same idea of predicting the BOLD signal using task predictors, but this time we added predictors that model the interaction between the seed region's activity and the experimental manipulation (Friston, Buechel, *et al.*, 1997; Poldrack *et al.*, 2011). An example of PPI result would be that the co-variation between the occipital cortex activity and activity in the posterior parietal cortex (PPC, a node of the dorsal FPAN) is more positive when a display comprises a salient distractor (SDD condition) compared with display without any salient stimuli (HD condition). A

critical aspect of PPI analyses is the fact that functional connectivity is better thought in terms of neuronal interactions than in terms of interactions between BOLD time series that are often noisy and which time courses are slow (thus not reflecting fast neural activity, and potentially representing the influence of multiple experimental events on brain responses). Consequently, the technical aspects of PPI have been improved since its beginnings (Friston, Buechel, *et al.*, 1997). This basically implies that the BOLD time series are "deconvolved" so that they resemble more a proper neuronal activity (i.e. the neuronal activity is tracked back from the BOLD signal) (Gitelman *et al.*, 2003). PPI allows us to estimate patterns of functional connectivity associated to experimental manipulations at the whole-brain level. This was important for our purpose, because we are very much interested in the brain networks underlying the processing of multiple/different priority signals and leading to a behavioral response. However, it does not provide any causal/directional information regarding the connectivity pattern.

In order to test more specific causal hypotheses about the interactions between the occipital cortex and dorsal FPAN, we made use of analyses of effective connectivity (Experiment 1). The PPI approach described above cannot tell us "what region sends information to another one", while effective connectivity can. Here, we used a particular kind of effective connectivity analysis called DCM, for dynamic causal modeling (Friston, Harrison, *et al.*, 2003). DCM is a Bayesian method that can be used to model the neuronal dynamics on the basis of fMRI time series (Friston, Harrison, *et al.*, 2003; K. Stephan *et al.*, 2010). DCM analyses generate brain responses data that can directly be interpreted in terms of connectivity strength between brain areas. It should be noted that the modeling of effective connectivity using DCM has a cost: to select a set of ROIs. As our main objective was to understand how the occipital activity pattern takes place under certain experimental conditions, we made use of the spatially-specific occipital ROIs (see figure 1.8C). To model the interaction between the occipital ROIs and the FPANs, we selected an additional ROI in the PPC. We did so because the role of the PPC in guiding attentional priority has been largely documented let it be for goal-directed attention (Gottlieb, 2007; Ptak, 2012; Vossel, Weidner, *et al.*, 2012; Geng, 2014; Vossel, Geng, *et al.*, 2014; Bisley & Mirpour, 2019), stimulus-salience (Buschman & Miller, 2007; Ptak, 2012), statistical learning (Melloni *et al.*, 2012; Won *et al.*, 2020; Zhang *et al.*, 2021) or reward (Anderson, 2016). In turn, we included a total of five ROIs in our effective connectivity analyses. In fact, DCM analysis requires the specification of multiple (physiologically plausible!) effective connectivity models a priori.

For example, one can compare a model where priority attribution in the occipital cortex (i.e. the pattern of activity taking place in the occipital cortex) does not involve the PPC (i.e. the occipital spatial activity is much likely to be due to "intra-occipital" interactions), with a model that involves a contribution of the connections between the occipital cortex and the PPC. To do so, one needs to specify the two models: 1) what

is the intrinsic effective connectivity pattern between the chosen ROIs (i.e. effective connectivity regardless of the tasks at hand), 2) where (which chosen ROI(s)) does the experimental condition "enter" the brain (e.g. the occipital cortex, for visual tasks) and 3) which connection of the intrinsic effective connectivity pattern (see 1) is modulated by which experimental condition. Once this is done, this specification is entered as a prior in the DCM analysis of the fMRI data. For each model, the DCM analysis estimates the probability of the data given the model. Then, this probability is compared between the different specified models (K. Stephan *et al.*, 2010) in order to choose a "winning model" (Bayesian model selection procedure). By doing so, the way attentional priority takes place in the occipital cortex can be estimated (again with the constraint of having to choose a restricted number of ROIs and of having to specify plausible biological models of brain connectivity).

Typically, in Experiment 1, we built dynamic causal models in order to test specific hypotheses regarding the mechanisms underlying the control of spatial attention in the presence of multiple attentional signals. We used analogous models to estimate the effect of priority signals on the effective connectivity between the occipital cortex and the PPC. Specifically, we aimed at addressing two main questions: i) Are parieto-occipital interactions "diffuse" (effective connectivity changes between the PCC and all the 4 occipital ROIs, implying that PPC distributes attentional priority to the entire occipital cortex); or "focused" (selective modulation of the connectivity between PCC and the occipital region that represents the target, i.e. ROI_IN); ii) Does the intra-occipital connectivity contribute to the formation of the distributed pattern of activity, and their modulation by the different priority signals, or not? This second question enabled us to address the issue of the relative contribution of feedforward/feedback signaling (cf. point i), above) versus any local computations/interactions within the occipital priority maps (e.g. salient distractor suppression).

Chapter 2

Experiment 1 - Dynamic causal interactions between occipital and parietal cortex explain how endogenous spatial attention and stimulus-driven salience jointly shape the distribution of processing priorities in 2D visual space

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KEYWORDS

attention, vision, space, connectivity, fMRI

HIGHLIGHTS

- We investigated the interplay between endogenous and exogenous spatial attention
- Distributed activity in occipital cortex represents current processing priorities
- Parietal top-down and occipital lateral signaling contribute to spatial selection

ABSTRACT

Visuo-spatial attention prioritizes the processing of relevant inputs via different types of signals, including current goals and stimulus salience. Complex mixtures of these signals engage in everyday life situations, but little is known about how these signals jointly modulate distributed patterns of activity across the occipital regions that represent visual space. Here, we measured spatio-topic, quadrant-specific occipital activity during the processing of visual displays containing both task-relevant targets and salient color-singletons. We computed spatial bias vectors indexing the effect of attention in 2D space, as coded by distributed activity in the occipital cortex. We found that goal-directed spatial attention biased activity towards the target and that salience further modulated this endogenous effect: salient distractors decreased the spatial bias, while salient targets increased it. Analyses of effective connectivity revealed that the processing of salient distractors relied on the modulation of the bidirectional connectivity between the occipital and the posterior parietal cortex, as well as the modulation of the lateral interactions within the occipital cortex. These findings demonstrate that goal-directed attention and salience jointly contribute to shaping processing priorities in the occipital cortex and highlight that multiple functional paths determine how spatial information about these signals is distributed across occipital regions.

2.1 INTRODUCTION

Visual scenes often contain more information than the brain can process at any given moment (Dukas, 2004). Visual selective attention allows prioritization of a subset of the incoming sensory signals and plays a key role in guiding overt behavior (Dukas, 2004; Chelazzi, Della Libera, *et al.*, 2011). Attention can be controlled via goal-directed mechanisms that account for the participant's goals (endogenous control), as well as via stimulus-driven mechanisms that relate to the physical characteristics of the external signals (exogenous control) (Desimone & Duncan, 1995; Egeth & Yantis, 1997). These two types of control mechanisms are traditionally associated with separate networks in the dorsal (associated to the control of endogenous attention) and ventral (associated to the control of exogenous attention) frontal and parietal areas (Corbetta, Kincade, *et al.*, 2000; Corbetta & Shulman, 2002). However, any real-life situation involves a complex mixture of signals likely to call upon both goal-directed and exogenous control (Itti & Koch, 2001; Chelazzi, Della Libera, *et al.*, 2011; Macaluso & Doricchi, 2013). Many different paradigms have been developed to study these interactions, including spatial cueing tasks combining central and peripheral cues (Berger *et al.*, 2005), search tasks with singleton distractors (Theeuwes, 1994; Belopolsky *et al.*, 2007) and more ecological approaches using naturalistic stimuli (Nardo *et al.*, 2016). At the behavioral level, performance improves when both endogenous and exogenous signals coherently prioritize the same location (i.e. salient targets, see Desimone & Duncan, 1995), while salient distractor stimuli presented away from the target location can hamper performance by exogenously pulling attention away from the target (Proulx & Egeth, 2007, but see Gaspelin & Luck, 2018, for the suppression of exogenous capture and Luck, Gaspelin, *et al.*, 2021, for a recent opinion paper on this issue). At the neural level, imaging studies found little impact of fully irrelevant salient distractors either in the dorsal or the ventral fronto-parietal network (Kincade, 2005; Indovina & Macaluso, 2007; Natale, C. A. Marzi, *et al.*, 2009; but see Thomsen *et al.*, 2005), showing instead that the activation of the ventral attentional system requires some combination of task-relevance and stimulus-driven salience (cf. "contingent capture of attention", Folk *et al.*, 1992; Natale, C. Marzi, *et al.*, 2010). These effects are consistent with the view that the ventral system acts as a "circuit-breaker", interacting with the dorsal system when attention needs to be re-oriented in a stimulus-driven manner towards a new relevant location (Corbetta & Shulman, 2002; Corbetta, Patel, *et al.*, 2008; Vossel, Weidner, *et al.*, 2012; but see Chica, Bartolomeo & Lupiáñez, 2013; DiQuattro, Sawaki, *et al.*, 2014; Vossel, Geng, *et al.*, 2014; for reviews).

Together with the fronto-parietal systems, attention control also entails the modulation of activity in the occipital visual cortex that represents the external visual space (Heinze *et al.*, 1994; Martínez *et al.*, 1999; Li, 2002; Seymour *et al.*, 2009; Awh *et al.*, 2012). The biased competition model of attention (Desimone & Duncan, 1995) proposes that the simultaneous presentation of multiple stimuli triggers competitive interactions

suppressing activity in the visual cortex and that attention can counteract this effect by enhancing activity for the attended stimulus and suppressing distractor-related responses. The theory was derived from single-cell data showing that both endogenous attention (Luck, Chelazzi, *et al.*, 1997; Reynolds, Chelazzi, *et al.*, 1999) and stimulus salience (Reynolds & Desimone, 2003) can reduce competitive interactions between two stimuli located within a neuron’s receptive field. Using functional Magnetic Resonance Imaging (fMRI), Kastner and colleagues reported related effects in the human visual cortex (Kastner, 1998; Kastner, Pinsk, *et al.*, 1999; Beck & Kastner, 2005). Competitive interactions were evidenced by comparing the simultaneous vs. sequential presentation of four stimuli briefly flashed in the same visual quadrant. In different studies, the authors demonstrated that both endogenous attention (Kastner, 1998) and exogenous factors (Beck & Kastner, 2005, using displays with/without singleton distractors) can reduce suppressive effects associated with the simultaneous presentation of the stimuli.

While highlighting the impact of both endogenous and exogenous attention on visual representations, these studies did not address the interaction between the two mechanisms of attention control. Only a few previous neuroimaging studies directly investigated how the presence of concurrent goal-directed and stimulus-driven signals affects the representation of visual space in the occipital cortex (Melloni *et al.*, 2012; Sprague *et al.*, 2018; Won *et al.*, 2020). These three studies utilized similar experimental approaches. First, a fMRI localizer was used to identify voxels in the occipital cortex that represent specific locations in the visual field (e.g. the four visual quadrants, in Melloni *et al.*, 2012). During the attention task, stimuli were presented simultaneously at multiple locations (the four quadrants, in Melloni *et al.*, 2012), but only one location was task-relevant and included the target to be judged. Across conditions, changes of the task-relevant location allowed us to map the spatial effects of endogenous attention orienting. At the same time, the physical characteristics of the stimuli (e.g. color or luminance) either at the task-relevant location or in one of the other locations (distractor locations) were also manipulated. The latter enabled studying how the endogenous and exogenous spatial attention control jointly influence activity in the visual cortex, as a function of the location of the two signals.

Overall, these three studies revealed a convergent pattern of results, including: i) increased activation in the occipital regions representing the target location (Melloni *et al.*, 2012; Sprague *et al.*, 2018; Won *et al.*, 2020), ii) increased activation in the occipital regions representing the location of salient compared with non-salient distractors (Sprague *et al.*, 2018; Won *et al.*, 2020), and iii) larger differences between target- and distractor-related activation, when the target was also the salient stimulus (Melloni *et al.*, 2012; Sprague *et al.*, 2018; Won *et al.*, 2020). The three studies thus confirmed that both endogenous and exogenous attention can modulate the visual cortex activity

in a spatially-specific manner and that the two types of control signals are combined in the occipital cortex. Yet, these studies did not explicitly assess how attention shapes processing priorities across the whole visual field (but see Sprague *et al.*, 2018, and the Discussion section). For example, is target priority also shaped by the activity in a non-target visual region laying within the same hemifield (i.e. yielding an overall hemifield bias)? More generally, can the joint effects of endogenous and exogenous attention be determined just by changes of activity in the region that represents the target, or is it the overall distribution of activity across the representation of the whole visual space that best accounts for visual selective attention?

Moreover, extensive evidence indicates that the modulation of activity in the visual cortex by endogenous attention arises from feed-back signals originating from the dorsal fronto-parietal network (Kastner, Pinsk, *et al.*, 1999; Moore & Armstrong, 2003). Exogenous effects in visual areas may also be mediated via dorsal regions that, following the initial detection of salient stimuli in the ventral system, would bias visual representations via feed-back connectivity (Corbetta & Shulman, 2002; Vossel, Weidner, *et al.*, 2012). However, exogenous attention may also be instantiated via direct interactions within visual cortex, including local competitive mechanisms (Chelazzi, Duncan, *et al.*, 1998; Reynolds, Chelazzi, *et al.*, 1999; Kastner, De Weerd, Pinsk, *et al.*, 2001), as well as via intra-areal lateral connectivity (Martínez *et al.*, 1999; Martin *et al.*, 2019, see also Turova & Rolls, 2019, for a computational model of spatial competition comprising inter-areal forward/feed-back connectivity). These different mechanisms emphasize again the importance of considering the overall distribution of attentional influence across the visual field (cf. also "priority maps" Ptak, 2012; Bisley & Mirpour, 2019) and raise the question of whether/how the fronto-parietal attention control network simultaneously modulates processing priorities at multiple locations of the visual field. In particular, this would relate to attention signaling from the posterior parietal cortex (PPC) to the visual occipital areas (e.g. see Buchel, 1997; Desseilles *et al.*, 2011; Vossel, Weidner, *et al.*, 2012).

To address these questions, we computed spatial bias vectors that combine fMRI activity across the occipital regions that represent the visual field, providing us with a measure of how spatial attention affects processing priorities in 2D space; and we used analyses of effective connectivity to test hypotheses about the mechanisms generating these distributed patterns of activity. During fMRI scanning, the participants were presented with 4 stimuli, one in each quadrant. On a trial-by-trial basis, a fully predictive central cue indicated the task-relevant quadrant, where the target was presented shortly thereafter. In three different display-conditions, the 4 stimuli were either all of the same color (homogeneous display, HD), the target was a salient color-singleton (salient target display, STD), or the distractor in the quadrant opposite to the target was a color-singleton (salient distractor display, SDD). The spatial bias vector for the HD-condition provides us

with a measure of the spatial distribution of processing priority generated by endogenous attention, while changes of the vector's magnitude and/or direction during STD and SDD index any further modulation by exogenous spatial attention. Dynamic Causal Models (Friston, Harrison, *et al.*, 2003; K. Stephan *et al.*, 2010) tested how the local connectivity within the occipital cortex and/or the connectivity between the occipital cortex and the PPC contribute to generating these distributed patterns of activity.

2.2 MATERIAL & METHODS

2.2.1 Participants

Twenty-four right-handed healthy adults were recruited for the study. They had normal or corrected-to-normal vision, no neurological, psychiatric or cognitive impairments and gave their written informed consent to participate in the study. The study was approved by a national ethics committee in biomedical research (Comité de Protection des Personnes: Sud-Méditerranée II, authorization ID: 2019-A00713-54). A total of nineteen participants were included in the final analyses (mean age: 27, range 20-39; 12 females). Five participants were excluded because: 1 participant asked to stop the experiment, for 1 participant we had technical problems with the eye-tracking, 1 participant had excessive head movements (> 3 mm), 1 participant moved the eyes towards the stimulus location during the localizer task (preventing us from obtaining the quadrant-specific ROIs) and 1 participant did not understand the task instructions (performance below chance level). While the final sample size ($N=19$) was not very large, a power analysis based on effect sizes reported in Won *et al.* (2020) (who employed a similar paradigm) permitted confirming that our study had sufficient statistical power. Specifically, we considered the effect of "salient vs. non-salient distractors" that was the weakest fMRI effect in our current dataset (cf. Results section, below). Using the G*Power software, we estimated the number of participants required to attain the power of 0.8, with $\alpha = 0.05$ and Won *et al.* (2020) effect size (Cohen's $d' = 0.757$). The resulting sample size was 16 participants, indicating that our study had sufficient power to detect this effect in the occipital cortex.

2.2.2 Experimental design

Each participant underwent a total of 7 functional imaging runs (6 runs of the main attention task, 7 min each; plus 1 localizer run, 10 min) and one anatomical scan (6 min). Visual stimuli were presented using Cogent Graphics, developed by John Romaya at the Wellcome Department of Imaging Neuroscience, running under MATLAB (The MathWorks, Natick, MA). The stimuli were projected on a screen placed at 90 cm from the participant's eyes (1024 x 768 pixels; projected image size: 31.5 cm height x 42 cm width).

Localizer task

The aim of the localizer was to identify the regions of the occipital cortex that represent the different locations of the visual field, where we then presented the stimuli during the main attention task (i.e. quadrant-specific ROIs). In order to maximize quadrant-specific activation, we employed high-contrast moving stimuli and asked the participants to perform a subtle discrimination of targets presented among distractors, employing a highly efficient blocked-design. The localizer stimuli consisted in a dynamic array of small bars (size = $0.5 \times 0.1^\circ$) moving at a speed of $28^\circ/\text{s}$ behind an aperture located in one of the four screen quadrants. The aperture was a $3 \times 3^\circ$ square centered at 7° of eccentricity from the display center (see Fig. 1, for an illustration; and online-video for an example of the localizer stimuli). The moving bars were seen through the aperture and were oriented horizontally or vertically, with the exception of the target-bars that were tilted of 45° to the right or to the left. The target-bars appeared at unpredictable times (range 1.08-3.24 sec) and the participants had to report the tilt orientation (right/left) by pressing a response-button with the index/middle finger of the right hand. At any one moment there were approximately 9 bars visible through the aperture. This procedure maximized both exogenous (densely packed moving stimuli) and endogenous (target discrimination among distractors) contributions in defining quadrant-specific activations and allowed us to identify the relevant spatial representations at the level of the individual participant (see Fig. 2A-B). The stimuli were presented in each screen quadrant for blocks of 14 seconds, interleaved with 12 seconds of central fixation without any visual stimulation. Each quadrant was stimulated 6 times, in a randomized order. The participants had to maintain central fixation throughout the localizer run.

Main attentional task

There were 6 fMRI runs comprising the main attention task. Each run included 84 trials. Each trial started with the presentation of a central cue signaling the task-relevant quadrant, where the target would appear shortly thereafter. The cue was a multi-colored circle in the style of a pie-chart. The cue was divided in 4 quarters, each with a unique color (blue, cyan, yellow and magenta; see Fig. 1). Before the experiment, each participant was assigned one specific color and was instructed to direct (endogenous) attention towards the quadrant indicated by the corresponding color. This procedure minimized any possible contribution of exogenous attention during the cueing phase. The cue (diameter = 0.5°) was presented for 1000ms and was followed by the presentation of the stimulus display. The display comprised 4 bars presented one in each quadrant (eccentricity = 7° , size = $2.0 \times 0.5^\circ$, see Fig. 1). The bar in the cued quadrant (target) was tilted to the left or the right side (45°) and the participant had to report the left/right tilt by pressing a response-button with the index/middle finger of the right hand. The bars in the other three quadrants (distractors) were oriented either horizontally or vertically and were fully

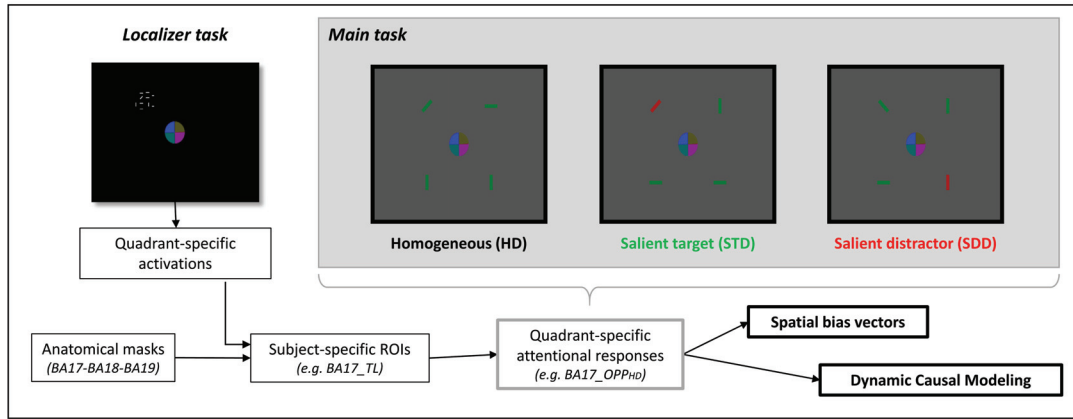


Figure 2.1: **Figure 1. Main steps of the data analysis and the three display conditions.**

First, subject-specific functional ROIs were generated by combining the fMRI responses during the localizer task with anatomically defined areas, using the AAL atlas. This resulted in 12 ROIs for each participant, corresponding to occipital regions in areas BA17, BA18, and BA19 that responded to stimuli in one visual quadrant (see also Fig. 2A-B). During the main attention task, the participant attended to one of the 4 quadrants, in 3 different display-conditions (see gray inset, and below). Activity for the resulting 12 conditions were averaged across ROIs, as a function of the represented quadrant and the attended location (see also Fig. 2B, panels on the right). This permitted assessing the effect of endogenous and exogenous attention at the level of the local activity in the three BA-areas (see Fig. 4 and Fig. S1B). In our main analyses, the ROIs activity was used to compute the “spatial bias vectors” (Figs. 3 and 5) and to test “Dynamic Causal Models” of effective connectivity (Figs. 6-7). The gray inset (“main task”) shows the three display-conditions that allowed us to investigate the interplay between endogenous and exogenous spatial attention; see also Fig. S1A, panels on the left. Each trial began with the presentation of a central cue that informed the participant in which quadrant the target would appear (100% validity, endogenous attention). The cue comprised four colored sectors. Before the experiment, each participant was instructed to direct attention towards the quadrant indicated by one specific color (blue, in the example). One second after the cue, the stimulus display was presented. This included 4 bars, one of which was the target (here, top-left) that required a left/right orientation discrimination. The other three distractor-stimuli were either vertically- or horizontally-oriented bars and were fully task-irrelevant. In different trials, one of the stimuli could be a color singleton (exogenous attention). This yielded to the three display-conditions: Homogeneous Display (HD), no singleton; Salient Target Display (STD), the target was the singleton; Salient Distractor Display (SDD), the distractor in the quadrant opposite to the target was the singleton. The three display-conditions were randomized and presented with equal probability. Note: the size of the cue is magnified for illustration purposes.

task-irrelevant. The stimulus display was presented for 300ms and the participant had up to 3000ms to respond. The inter-trial interval was between 3000 and 4000ms (uniform distribution). The participants had to maintain central fixation throughout the trial.

In different trials, the 4 bar-stimuli were either all of the same color (green or red, counterbalanced across participants) or included a color singleton (one green bar among

three red bars, or vice-versa). Because of technical difficulties to accurately measure luminance inside the MR bore, we adjusted the luminance of the green and red stimuli outside the scanner (luminance of both colors = 13.5cd/m^2). Most likely, the absolute luminance values of the stimuli projected in the scanner were quite different, but the relative luminance of the green and red stimuli - which was the relevant parameter here - should remain relatively unaffected. The presence/absence and the location of the color singleton yielded three display-conditions (see Fig. 1; "Main task", in the gray inset): Homogeneous Display (HD, all stimuli of the same color), Salient Target Display (STD, when the target was the color singleton) and Salient Distractor Display (SDD, when the distractor stimulus in the quadrant opposite the target was the color singleton). The three display-conditions were presented with equal probability.

The combination of the 4 target-locations and 3 display-conditions led to a total of 12 experimental conditions that were presented in an unpredictable order and that, across the 6 runs, were repeated 42 times each. These 12 conditions conform to a 4×3 full factorial design manipulating in an orthogonal manner the endogenously attended location (4 cued/target quadrants: TL, top-left; TR, top-right; BR, bottom-right; BL, bottom-left) and exogenous attention (3 display-conditions: HD, no exogenous signals; STD, exogenous signal at the same location as endogenous attention; SDD exogenous signal at the opposite location compared to the target); see also Fig. S1.

2.2.3 Eye tracking

Participants' gaze-direction was tracked during the whole imaging session using a MR-compatible EyeLink 1000 (SR Research Ltd., Mississauga, Ontario, Canada) at a sampling rate of 500Hz. At the start of the session, the system was calibrated with a 5-point procedure. The calibration points were located in the four quadrants at 7° eccentricity, plus the center of the screen. The analyses of the eye-tracking data were carried out with custom scripts in MATLAB. Eye-tracking data were down-sampled to 100Hz. For each trial, the gaze-data were extracted in a 2500ms window, starting 500ms before cue onset. The data were baseline-adjusted using the median of the vertical and horizontal position during a 500ms pre-cue period. We evaluated the quality of each trace considering the percentage of data-points with values larger than 10° or smaller than -10° , typically caused by blinks or poor/noisy signal. Trials with more than 50% of reliable data-points (86% of the total) underwent further analyses to detect any loss of central fixation. We first identified new fixations as any displacement of the gaze-position larger than 0.5° and lasting for at least 100ms. Trials containing any fixation outside a central box ($\pm 2^\circ$ from the center of the screen) were classified as "fixation-loss". These trials (5% of the trials with reliable data) were excluded from the behavioral analyses and were modeled in a separate regressor of no-interest in the fMRI analyses.

2.2.4 Behavioral analyses

The analysis of the reaction times (RT) for the attention task made use of a linear mixed model analysis using log-transformed RTs implemented in R-studio (Bates *et al.*, 2015). Trials with wrong/no/late responses and/or including losses of fixation (cf. above) were discarded from the analysis. The model included the log-transformed RTs as the dependent variable and the display-condition as the explanatory variable (with 3 levels: HD, STD SDD). Because of the repeated measures, the model also included subject-specific intercepts. It is important to note that in the current design, all trials included 100% valid cues and the manipulation of endogenous attention concerned solely the position of the target (cf. Fig. S1A, panels on the left). Accordingly, we did not expect any behavioral correlate of endogenous attention and averaged the RTs associated with targets in the 4 quadrants before submitting the behavioral data to the statistical models. Concerning the effect of exogenous attention (i.e. display-condition), salient target (STD) may speed up RTs compared to HD (no salient signals), while salient distractors (SDD) may slow down responses. Nonetheless, it should be anticipated that the use of 100% valid cues (highly focused endogenous spatial attention) is likely to reduce/suppress the impact of exogenous salience on behavioral performance (see Luck, Gaspelin, *et al.*, 2021; Rashal *et al.*, 2022, and Discussion section). The accuracy data were not analyzed, because the orientation-discrimination performance was at ceiling ($> 95\%$, in all conditions) most likely reflecting the use of fully-predictive 100% valid cues.

2.2.5 Image acquisition and preprocessing

T2*-weighted echoplanar images (EPI) with blood oxygen level-dependent (BOLD) contrast (interleaved multiband sequence, multiband factor = 2, 50 slices covering the entire brain, field of view = 220x210.4mm, repetition time = 1.72s, echo time = 30ms, phase encoding direction = antero-posterior, slice orientation = approx. axial, voxel size = $2.4 \times 2.4 \times 2.4\text{mm}^3$) were obtained using a 3T MRI System (Trio, Siemens). A high-resolution anatomical scan was acquired using a standard T1-weighted 3D MP-RAGE sequence (repetition time = 3s, echo time = 3.8ms, inversion time = 1.1s, sagittal 3D volume with a field of view of 224x256x192mm, voxel size = $1 \times 1 \times 1\text{mm}^3$). The functional data were preprocessed and analyzed with Statistical Parametric Mapping software SPM12 (Wellcome Department of Imaging Neuroscience, University College London, UK; <http://www.fil.ion.ucl.ac.uk/spm>). After discarding the first four volumes of each imaging run, images were corrected for head movements. Slice-acquisition delays were corrected using the middle slice as reference. All images were normalized to the SPM12 Tissue Probability Map and re-sampled to 2mm isotropic voxel size. Unsmoothed data were used in all the analyses.

2.2.6 Single-subject analyses

Localizer and individual Regions Of Interest (ROIs)

The localizer data served to identify, for each participant, the voxels in the occipital visual cortex that responded preferentially to stimuli presented in each quadrant (Fig. 1 and Fig. 2A-B). The single-subject general linear model (GLM) included the 4 conditions of interest related to the location of the visual stimuli (top-left: "TL", top-right: "TR", bottom-right: "BR" and bottom-left: "BL") modeled as blocks of 14 seconds and convolved with the canonical Hemodynamic Response Function in SPM12, plus the 6 movements parameters resulting from the realignment procedure, as regressors of non-interest.

We used a combination of functional contrasts and the Automated Anatomical Labeling atlas (AAL, Tzourio-Mazoyer *et al.*, 2002) to identify quadrant-specific responses in anatomically-defined occipital areas BA17, BA18 and BA19. Please note that here we refer to these spatially-specific responses as "quadrant-specific", because only four positions were tested (as opposed to the entire visual field), and that these should be considered in retino-centered coordinates, because eye-position was held fix and carefully controlled during both the localizer and the main experiment. For each participant, using the functional localizer data we tested for the main effects of side at the whole-brain level (e.g.: "TL+BL > TR+BR", for left hemifield quadrants) and separated voxels responding to the upper or the lower quadrant using inclusive masking with the relevant simple main effect (i.e. top-left quadrant: "TL > BL", and bottom-left quadrant: "BL>TR"). All contrasts were thresholded at $p\text{-unc.} = 0.005$, which was the sole decision parameter finally determining the number of voxels in each ROI (see table S1 for the average number of voxels comprised in each occipital ROIs). This initial whole-brain threshold typically resulted in multiple activation clusters in the hemisphere contralateral to the simulated quadrant, comprising both dorsal and ventral extrastriate visual cortex, as well as the calcarine fissure; see Fig. 2A, for an example. These subject-specific activation clusters were then split based on anatomical criteria using the AAL atlas, finally yielding to 12 ROIs for each participant (4 visual-quadrants x 3 BA-areas), see Fig. 2B. We labelled these ROIs on the basis of their spatial selectivity and BA-area. For example, "ROI18_TL" refer to the ROI in area BA18 responding to stimuli in the top-left quadrant, which includes voxels located in the right ventral occipital cortex. The average size of the quadrant-specific ROIs (mean number of voxels \pm SEM) was: 82.24 ± 6.33 for BA17, 220.03 ± 15.67 for BA18 and 187.92 ± 15.24 for BA19 (see also table S1).

In addition, for each participant, we identified voxels in the PPC that activated during the localizer task irrespective of the stimulated quadrant ("ROI_PPC"). For this we considered the omnibus F-test at $p\text{-unc.} = 0.001$ and retained voxels belonging to area BA7 using the AAL atlas (Tzourio-Mazoyer *et al.*, 2002). The parietal ROI comprised

voxels in both hemispheres and, on average across voxels, it responded to stimulation of all the four visual quadrants (see Fig. 2C, and table S1 for the number of voxels in the ROI_PPC; see also Discussion section concerning the possible differential role of the left and right PPC). The ROI_PPC was used for the analyses of effective connectivity.

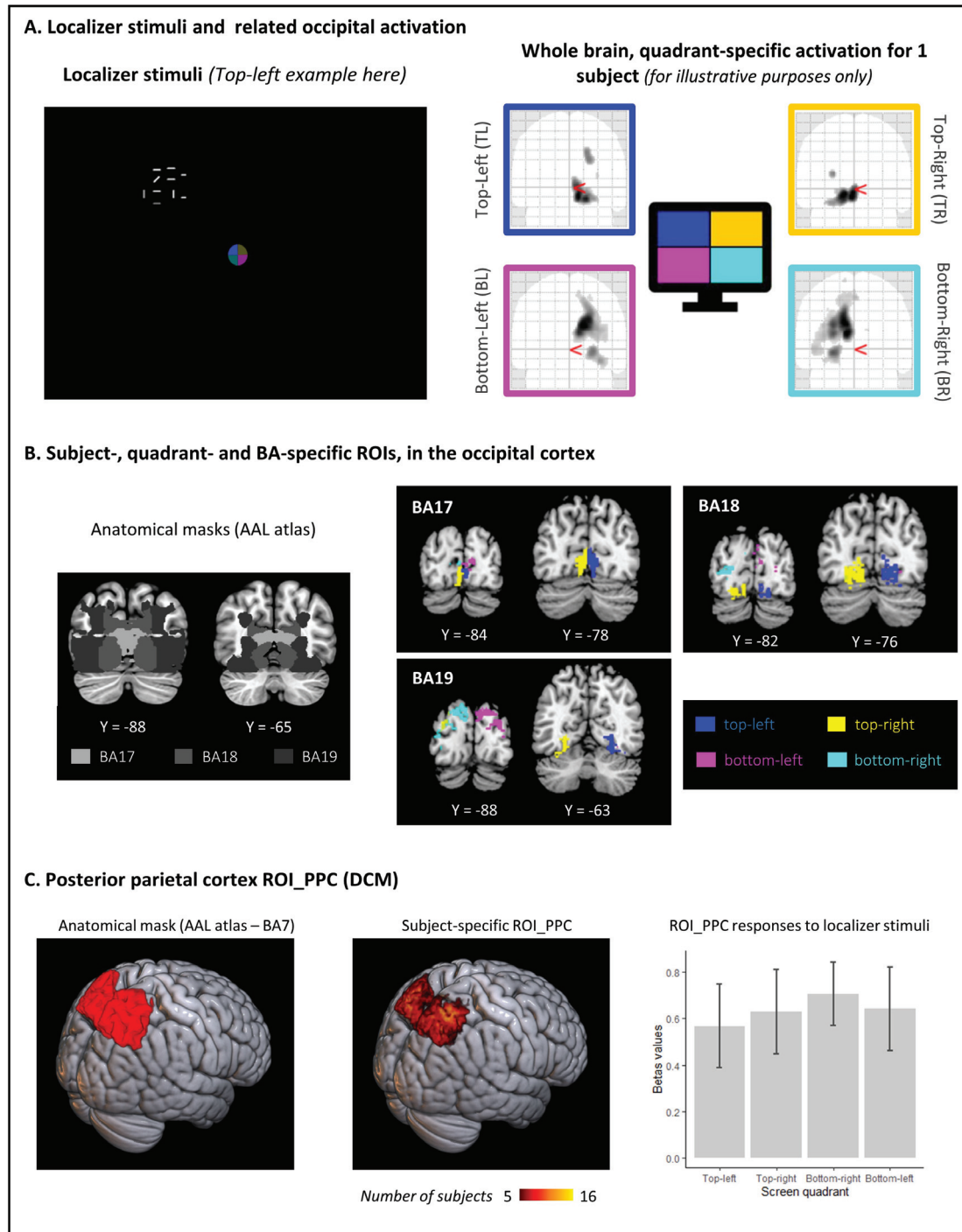


Figure 2.2: **Figure 2. Localizer task and ROIs definition.**

A - Localizer stimuli and the corresponding quadrant-specific activation in the occipital cortex. The left panel shows an example of the localizer stimuli (see also online-video). Localizer stimuli were presented using a blocked-stimulation protocol. For each block, a set of small white moving bars appeared in only one of the 4 quadrants of the screen (here in the top-left quadrant). The right panel shows an example of the whole brain results for one participant. Using a combination of functional contrasts (see Methods section), we identified voxels showing quadrant-specific responses during the localizer task. The 4 maximum intensity projections highlight multiple clusters associated with stimulation of each visual quadrant (cf. color coding). **B** - Subject-, quadrant- and BA-specific ROIs in the occipital cortex. The left panel show the anatomical masks (from the Automated Anatomical Labeling atlas) used to partition the functionally defined quadrant-specific responses (see panel A) into anatomically-defined BA17, BA18 and BA19. For each participant this enabled us to define 12 separate ROIs, corresponding the 4 quadrant-representations in the 3 BA areas. The right panels show the localization of the final ROIs, highlighting voxels where there was an overlap of at least 3 participants. **C** - The ROI in the posterior parietal cortex. The leftmost panel shows the anatomical mask (also from the Automated Anatomical Labeling atlas) used to define the ROI_PPC. Individual ROI_PPC were created by combining functional data (activation irrespective of stimulated quadrant, during the localizer task) and this anatomical mask. The central panel shows the localization the ROI_PPC across participants. The rightmost panel shows the mean \pm SEM beta values of the ROI_PPC separately for each four quadrant-specific stimulations during the localizer.

Main task

The single-subject GLMs for the main task comprised 12 conditions of interest corresponding to the initial 4 x 3 factorial design: 4 target-quadrants x 3 display-conditions (HD, STD, SDD; see also Fig. S1A, panels on the left), plus one predictor including trials to be excluded from the group analyses (no response, incorrect orientation-discrimination, reaction time out of the 200-3000ms response window and fixation-loss trials, cf. above), and 6 regressors with the realignment parameters. The GLMs included the 6 fMRI runs, with separate predictors for each run. Each trial was modeled using the canonical Hemodynamic Response Function in SPM12. The event-onsets were time locked to the presentation of the stimulus display and the event-duration was 300ms. We made this choice, rather than time locking to the cue-onset, in order to maximize the likelihood of capturing the combined effects of both the endogenous cue and the stimulus-array. Only the parameter estimates of the 12 conditions of interest were used for the subsequent group-level analyses.

2.2.7 Group-level analyses

Target- and salience-related local activation

The first question that we asked was how endogenous and exogenous attention jointly affect local activation in the occipital visual cortex. For this, we examined the activity in the ROIs representing the target quadrant and the opposite quadrant, where the

salient distractors were presented in the SDD display-condition (see Fig. S1B, panel on the left). First, separately for each subject and the 12 ROIs, we averaged the parameter estimates across sessions and voxels, separately for the 12 conditions of interest. Next, for each BA-area, we averaged the data across the 4 quadrant-specific ROIs as a function of the target-location (Fig. S1A, panels on the right). Separately for the 3 display-conditions, we computed the activity associated with the presentation of the target in the visual quadrant represented by the ROI (ROI_IN responses) and activity when the target was in the opposite quadrant (ROI_OPP). For example, to obtain the "ROI_OPP" responses in area BA17, we averaged the activity of the ROI17_TL when the target was in bottom-right quadrant, ROI17_TR when the target was bottom-left, ROI17_BR when the target was top-left, and ROI17_BL when the target was top-right. This produced a single value per subject for each condition (IN/OPP), BA-areas and display-condition. It is important to stress that this averaging procedure preserved the orthogonality between the endogenous factor (cued/target location) and exogenous factor (salience) of the experimental design; see Fig. S1B, rightmost panel.

It should be noticed that for the salient-distractor display (SDD), the response in ROI_OPP corresponds to the activity when a salient distractor is presented in the quadrant represented by the ROI. By contrast, the ROI_IN responses in the salient-target display (STD) correspond to the activation associated with a salient target (cf. Fig. S1B, panel on the left). Accordingly, using the ROI_IN and ROI_OPP responses in the SDD and STD display-conditions we could test for the effect of endogenous attention ($ROI_IN_{STD} + ROI_IN_{SDD} > ROI_OPP_{STD} + ROI_OPP_{SDD}$), the effect of exogenous attention ($ROI_IN_{STD} + ROI_OPP_{SDD} > ROI_IN_{SDD} + ROI_OPP_{STD}$) and their interaction, as fully independent factors. A 2x2x3 repeated-measure ANOVA with the factors: quadrant-type (spatial endogenous attention: ROI_IN, ROI_OPP) x display-condition (spatial exogenous attention: STD, SDD) x BA-area (BA17, BA18, B19) was employed to assess these effects. It should be noticed that because the salient-singleton was presented in the ROI_IN during STD, but in the ROI_OPP during SDD, the effect of exogenous attention corresponds to the interaction between the factors "quadrant-type" and "display-condition" (i.e.: $ROI_IN_{STD} + ROI_OPP_{SDD} > ROI_IN_{SDD} + ROI_OPP_{STD}$).

Spatial bias vectors and gain/cost indexes

The analyses described in the previous section allowed us to test whether the response of quadrant-specific occipital ROIs increased when the represented quadrant contained a target compared to when the target was in the opposite quadrant (ROI_IN vs. ROI_OUT, i.e. a spatially-specific effect of endogenous attention), and whether this was modulated by the location of the salient singleton (STD vs. SDD, corresponding to the spatial interaction between endogenous and exogenous attention). However, these

analyses do not fully capture the spatial distribution of the attentional effects, because they discard information about the activity in the ROIs that represent visual locations without any target or salient distractor (i.e. activity in the contralateral hemifield, but in the same upper/lower quadrant as the target: "ROI_CONTRA", and activity in the same hemifield as the target, but in the other upper/lower quadrant: "ROI_IPSI"). For example, directing endogenous attention to the top-left quadrant may generate a spatial bias across the entire left hemifield rather than specifically boosting activity in the ventral occipital cortex that represents the top-left quadrant.

In order to capture these effects, we computed spatial bias vectors that combine the activity of all four quadrant-specific ROIs (IN, OPP, CONTRA and IPSI, separately for each BA-area) and that represent the direction and the strength of the attentional bias in 2D visual space (see Fig. 3). First, we calculated condition-specific biases as the Euclidian sum of 4 vectors, each representing the activity of one ROI ("attention top-left", in Fig. 3A). All vectors originated at the (0,0) coordinates, i.e. the center of the visual field (no bias), but with different directions corresponding to the quadrant represented by the ROI (e.g. (-1,1) for the ROI_TL) and a magnitude corresponding to the activity of the ROI. The Euclidian sum of the 4 vectors quantified the direction and the strength of the attentional bias for one condition, in the relevant occipital representation (i.e. BA17, BA18 and BA19). Next, for each subject and display-condition, we computed the spatial bias vectors by averaging the data across the four target-quadrants (see Fig. 3B). For this, the condition-specific vectors were first projected into the top-left quadrant and then averaged to obtain the final spatial bias vectors associated with each display condition: \overline{biasHD} , $\overline{biasSTD}$ and $\overline{biasSDD}$. In this frame of reference, negative x-values indicate a bias towards the hemifield of the target, and positive y-values indicate a bias towards the upper/lower target location. Please note that, in these displays/frames of reference, the IPSI and CONTRA labels refer to the location of the target and not some anatomical location in the occipital cortex (vectors are computed using the signal of the 4 ROIs, in both hemispheres). For example, if a hypothetical spatial bias vector has direction (-1, 0), i.e. lying on the x-axis and pointing leftward without any difference between "IN" and "IPSI" quadrants, this would mean that the BA-area is modulated according to the target hemifield, but not the up/down direction of attention.

We examined the geometrical characteristics of the spatial bias vectors to assess the impact of the display-condition on the spatial distribution of attention, as represented in BA17, BA18 and BA19. First, for the HD condition we tested whether the magnitude of the bias vector was larger than zero ($|\overline{biasHD}| > 0$), indicating the presence of an endogenous spatial bias; and whether the vector-direction corresponded to the target location (i.e. 45° top-left, cf. dotted-line in Fig. 5, plots on the right: $\text{angle}(\overline{biasHD}) - 45$, different from 0).

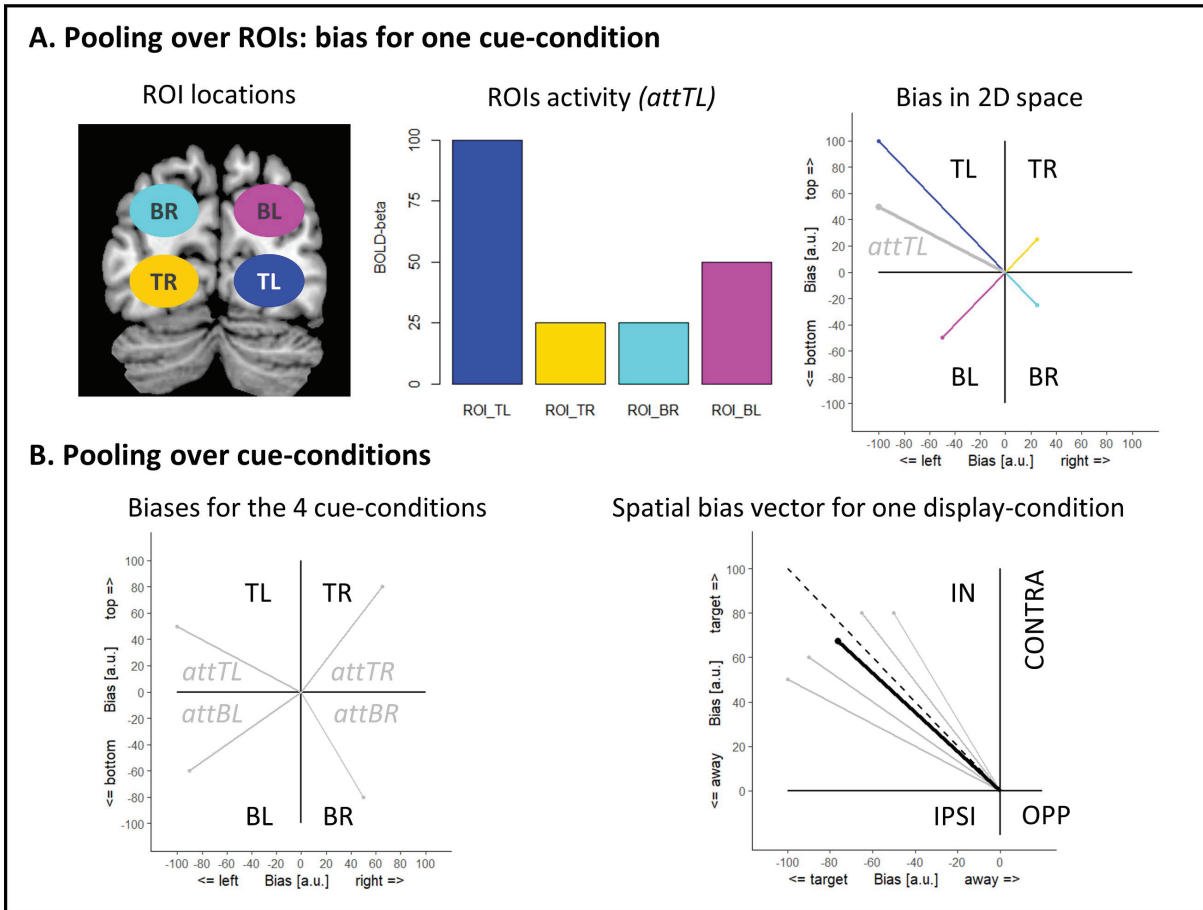


Figure 2.3: **Figure 3. Illustration of the procedure for the computation of the spatial bias vectors.**

A - Computation of the 2D bias-vector for one condition (here attention top-left, HD), considering the BOLD activity in the 4 ROIs that represent the 4 quadrants in one BA-area. The leftmost panel illustrates the ROIs location (BR = ROI representing the bottom-right quadrant, etc. cf. also Fig. 2B). The central panel displays the activity in the 4 ROIs, during the relevant condition (*attTL*). The rightmost panel shows the projection of the activity of the 4 ROIs in 2D space (cf. colored vectors) and their sum that yields the bias-vector for this condition (in light gray). In this illustrative example, attention to the top-left quadrant generates a bias towards the attended quadrant (TL), but also a more general left-hemifield bias due to the high activity in the ROI that represent the bottom-left quadrant (cf. magenta bar in the central panel). **B** - Illustration of the bias-vectors (computed as in panel A) for the four cue-conditions: *attTL*, *attTR*, *attBR*, *attBL*. The panel on the right shows the final spatial-bias vector. The 4 condition-specific vectors are projected to a new frame of reference, where the top-left locations represent the quadrant of the target (IN), bottom-right locations represent the quadrant opposite to the target (OPP), and the other two quadrants represent IPSI and CONTRA, with respect to the target position. The dotted line indicates the direction of the target, in this frame of reference. The 4 condition-specific vectors (light gray) are averaged yielding the final spatial-bias vector for this display condition (in black). In this example, the vector lies below the diagonal (dotted line) signifying the presence of an overall bias towards the target hemifield, which comprises both the “IN” (target) quadrant and the “IPSI” quadrant. The spatial-bias vectors were computed for each subject and BA-area, separately for the 3 display-conditions (see Fig. 5). L/R: left/right; T/B: top/bottom. OPP/CONTRA/IPSI: opposite/contralateral/ipsilateral with respect to the target quadrant (IN).

Next, we investigated the influence of exogenous attention by testing for changes of magnitudes and directions for "STD vs HD" (effect of salient targets) and "SDD vs. HD" (effect of salient distractors). We expected that salient targets would strengthen the bias towards the target location ("Gain_indexes"), while salient distractors would weaken this bias ("Cost_indexes"). For magnitudes, we considered the magnitude difference of the two vectors ($\text{Gain_mag} = \|\overline{\text{biasSTD}}\| - \|\overline{\text{biasHD}}\|$; and $\text{Cost_mag} = \|\overline{\text{biasSDD}}\| - \|\overline{\text{biasHD}}\|$). We expected positive values for Gain_mag and negative values for Cost_mag, corresponding to stronger/weaker spatial biases for STD/SDD compared with HD. For the vector directions, we assessed whether the salient stimuli modified the pointing direction of the spatial bias vector. This was tested as the difference between the deviation of the bias vectors with respect to the target location, in "STD vs. HD" and "SDD vs. HD" ($\text{Gain_dir} = (\text{angle}(\overline{\text{biasSTD}}) - 45) - (\text{angle}(\overline{\text{biasHD}}) - 45)$; and $\text{Cost_dir} = (\text{angle}(\overline{\text{biasSDD}}) - 45) - (\text{angle}(\overline{\text{biasHD}}) - 45)$). All the indexes were calculated at the single-subject level, separately for BA17, BA18 and BA19, and submitted to a series of one-tailed one-sample t-tests.

We then assessed the behavioral relevance of the measured effects using two separate multiple regression models that included the participants' RT as the dependent measure (Gain-regression: $\text{RT}_{STD} - \text{RT}_{HD}$; Cost-regression: $\text{RT}_{SDD} - \text{RT}_{HD}$) and the Gain_mag/Cost_mag fMRI indexes computed in the 3 BA-areas as predictors. The analyses were implemented using the fitlm-function in MATLAB, with "robust" estimation option.

2.2.8 Dynamic causal modeling (DCM)

The aim of the DCM analysis was to test specific hypotheses about the effect of attention on the effective connectivity of the occipital cortex and the PPC (see "model space", below). In order to constrain the number of nodes in the dynamic causal models, the models included the 4 quadrant-specific ROIs in BA18 (which showed the most robust effects in the vector analyses described above) and one region in the PPC (ROI_PPC). The PPC was selected because of the extensive literature pointing to this region as the main source of attention signals that modulate activity in the occipital cortex (see Introduction and Discussion sections). The ROI_PPC comprised the voxels in area BA7 that activated during the localizer scan irrespective of the stimulated quadrant.

For the DCM analyses of effective connectivity, a new set of single-subject GLMs was constructed. The 6 fMRI runs of the main attention task were concatenated and the GLM now contained 17 regressors of interest: the 12 experimental conditions (3 display-conditions x 4 target-quadrants, correct trials only), four regressors modeling the salient color-singleton separately for each quadrant, but irrespective of whether the singleton was a target or a distractor, plus one regressor that included all trials of the experiment. This

GLM enabled us to then define the driving input to the DCMs (i.e. the regressor including all trials/display-onsets, and regressors coding for the position of the singleton) and the modulatory parameters of the DCMs (i.e. the 3 display-conditions, see also below). Additional regressors were added to model the main effect of fMRI run, error/fixation-loss trials and the realignment parameters.

Specification of the DCM and the model space

In DCM, three sets of parameters (A, B, C) characterize the connectivity of the network (Zeidman *et al.*, 2019). The A-parameters specify the intrinsic connections between the nodes, regardless of the experimental condition. Here, we allowed all possible connections between the 5 ROIs. The C-parameters specify the driving inputs to the model. Here, the driving input affected only the 4 quadrant-specific occipital ROIs. All four ROIs were driven by the regressor coding for "all trials", because each trial included visual stimuli in the 4 quadrants, plus one singleton-regressor accounting for the presence of a salient stimulus in the ROI's quadrant (see also K. E. Stephan *et al.*, 2007, who used an analogous approach when addressing the effect of endogenous attention on the connectivity between the occipital cortex and the posterior parietal cortex).

The B-parameters specify which experimental conditions can modulate the directional influence of one region onto another and constitute the main parameters of interest in the current DCM analysis. To test our hypotheses concerning the role of the connectivity between occipital regions and between the occipital cortex and the PPC, we constructed 6 models. The models were partitioned in two families (K. Stephan *et al.*, 2010). In family F1, all the 12 attention conditions modulated feed-forward and feed-back connections between the PPC and all 4 occipital ROIs. By contrast, in family F2 the experimental conditions could affect only the connectivity between the PPC and the occipital ROI representing the location of the target (ROI_IN), and did so only when endogenous attention was directed towards that quadrant. For example, the connectivity between ROI_PPC and ROI18_TL was modulated only when endogenous attention was directed top-left, with 3 separate B-parameters accounting for the effect of display-condition (i.e. presence and location of the salient singleton). Within each family, 3 models embodied our hypotheses about the role of occipital-occipital connections. In particular, we sought to test alternative/complementary explanations to the changes of activity in the 4 occipital ROIs, beside their interactions with the ROI_PPC. Because our main interest was to understand how the brain selects pertinent information in the target-quadrant (plus how salience affects this), the model space put emphasis on the connectivity of the relevant ROI_IN. Accordingly, the first model comprised the modulation of all the connections between the occipital ROIs by all 12 experimental conditions. In the second model, attention could modulate only the connections "from" and "to" the ROI_IN that represents the current target location, and only conditions with endogenous

attention directed towards the ROI quadrant could modulate these connections (three B-parameters corresponding to the 3 display-conditions). Finally, in the third model attention did not modulate any of the lateral connections between the occipital ROIs.

This model space can be seen as a 2x3 design: the 2 families tested whether the effect of attention on the occipital-PPC connectivity was "spatially diffused" (i.e. involving the occipital representation of the entire visual field, F1) or "spatially focused" (i.e. related only to the representation of the currently relevant quadrant, F2), and the 3 models within each family tested an analogous effect related to quadrant-specificity, but now considering the lateral connectivity within the occipital cortex. The full DCM model space is illustrated in Fig. 6.

Model selection and parameter inference

Given that our participants pool was sampled from a homogeneous population of young healthy adults and that the task involved simple visual judgments, we assumed that the optimal model structure would be the same across participants. Thus, a fixed-effects Bayesian model selection (BMS-FFX) was conducted to identify the most probable family and the most probable model (K. Stephan *et al.*, 2010). The selection procedure takes into account the models' complexity (here the number of B-parameters that enable changes of connectivity as a function of the experimental conditions), penalizing more complex models, and selecting the best compromise between accuracy and complexity (Penny *et al.*, 2004; Friston, Mattout, *et al.*, 2007). We then used fixed-effect Bayesian Parameter Averaging (BPA) (K. Stephan *et al.*, 2010) on the winning model to test for condition-specific changes of the connectivity B-parameters. Specifically, we implemented an averaging strategy analogous to that described above for the effects of conditions on the ROI activity (cf. Fig. S1). Briefly, we averaged the B-parameters as a function of the target position/endogenous attention (ROI_IN, ROI_OPP, ROI_CONTRA and ROI_IPSI) and assessed the effect of exogenous attention by comparing "STD vs. HD" (salient targets) and "SDD vs. HD" (salient distractors). We discuss attentional modulations with posterior probabilities $> 95\%$.

Data availability statement

Processed imaging data are available on the EBRAINS platform: <https://search.kg.ebrains.eu/instances/cd4c0231-f9d6-4964-9763-54347029dd00>.

2.3 RESULTS

2.3.1 Behavioral data

The target orientation-discrimination task was very easy, with an average accuracy $> 95\%$, in all three display conditions. Because of this the behavioral analyses considered only the response times (RTs). The average RTs numerically matched the expected pattern, with the fastest RTs for salient targets (STD; mean \pm SEM = 584 ± 26 ms), intermediate RTs for the homogeneous display (HD; 589 ± 30 ms) and the slowest responses when the display included a salient distractor (SDD; 596 ± 31 ms). Based on this qualitative pattern, we carried out a linear mixed model analysis using log-transformed RTs that revealed a significant effect of display condition ($F(2, 8804) = 3.68, p = 0.033$). We should stress that, albeit statistically significant, the effect of salient item’s location was small (12ms, for STD vs. SDD; fixed-effect Cohen’s $d = 0.03$) and should not be over-interpreted. This behavioral effect may reflect some combination of exogenous capture and distractor suppression (cf. Luck, Gaspelin, *et al.*, 2021, and Discussion section); but please note that our aim here was to investigate how quadrant-specific occipital ROIs and the posterior parietal cortex jointly process endogenous and exogenous spatial signals, rather than assessing the specific constraints that might determine any residual distractor-effects at the behavioral level.

2.3.2 Target- and salience-related local activation

We first aimed to assess the effects of endogenous and exogenous spatial attention considering activity in the ROIs representing the target quadrant and the opposite quadrant, as a function of display-condition (see also Fig. S1B, on the left) and BA-areas. The corresponding $2 \times 2 \times 3$ (ROI_IN/ROI_OPP \times STD/SDD \times BA17/18/19) ANOVA revealed a significant main effect of quadrant ($F(1,198) = 111.9, p < 0.001, \eta^2 p = 0.36$), with larger activity in ROI_IN compared to ROI_OPP, corresponding to the effect of endogenous spatial attention. The analysis revealed also an interaction between quadrant and display-condition ($F(1,198) = 5.3; p = 0.021; \eta^2 p = 0.03$), with larger activity in ROI_IN_{STD} compared to ROI_IN_{SDD} and in ROI_OPP_{SDD} compared to ROI_OPP_{STD}. This corresponds to the spatial effect of salience/exogenous attention, because the singleton item was presented in the ROI_IN in STD, while it was presented in the ROI_OPP in SDD, see also Methods section above and Fig. S1B. There was a main effect of BA-area ($F(2,198) = 35.4; p < 0.001; \eta^2 p = 0.26$, with BA19 showing the highest activation), but no other main effects or interactions (all p -values > 0.5 , all $\eta^2 p < 0.01$). The results thus indicate that while both endogenous and exogenous attention affected activity in the three occipital visual areas, the two types of attention signals did not significantly interact (see Discussion section).

Fig. 4 shows the averaged parameters estimates in the ROIs representing the target

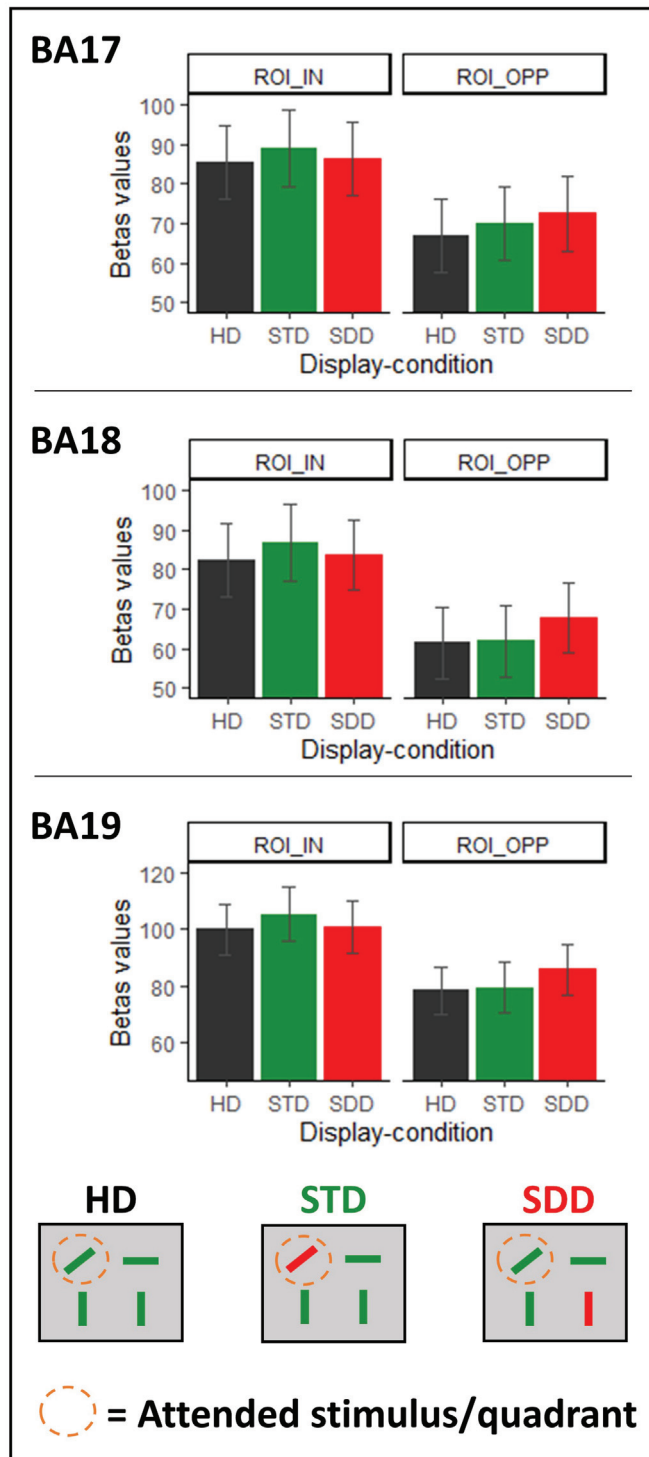


Figure 2.4: **Figure 4. Attentional effects in BA17-BA18-BA19.**

Local activity during the main attention task averaged across the 4 ROIs belonging to each BA-area, as a function of the represented quadrant (ROI_IN, ROI_OPP) separately for the 3 display-condition (HD, STD and SDD), see also Fig. S1. The data analysis revealed an effect of endogenous spatial attention, an effect of exogenous attention, but no significant interaction between the two types of attention control signals. Plots show mean beta values \pm SEM. See also Fig. 2 for the anatomical localization of these regions.

quadrant (ROI_IN) and the opposite quadrant (ROI_OPP), as a function of display-conditions and BA-areas. The larger activity in ROI_IN (bars 1-3) compared with ROI_

OPP (bars 4-6) highlights the effect of endogenous spatial attention. The main effect of salience, which by design is orthogonal to the effect of endogenous spatial attention (cf. Fig. S1), is expressed by maximal activity for the STD condition in the ROI_IN (i.e. when the represented target was also the salient color-singleton, see bar 2 in each plot) and for the SDD condition in the ROI_OPP (i.e. when a salient distractor was shown in the represented quadrant, see bar 6 in each plot).

2.3.3 Spatial-bias vectors and gain/cost indexes

The data of the ROI_IN and ROI_OPP highlighted that both endogenous and exogenous attention affect the distribution of processing priorities towards/away from these two locations. However, these analyses do not consider the contribution of the occipital regions representing other locations of the visual field (ROI_CONTRA and ROI_IPSI). In order to take these into account, we computed spatial bias vectors using the distributed activity across all 4 ROIs and tested how endogenous and exogenous attention affect the magnitude and the direction of these vectors (Fig. 5; see also Fig. 3 for a detailed illustration of how the bias vectors were computed).

First, we assessed the effect of endogenous attention by testing whether the vectors' magnitudes in the HD condition were different from zero ($||\overline{biasHD}|| > 0$). This revealed highly significant effects in the 3 BA-areas (all p-values < 0.001 , all Cohen's d > 3.02). The direction of the vectors provides us with the additional information about how each area implements the endogenous bias in 2D space. In our arbitrary frame of reference, the location of the target was set to $[-1 \ 1]$, that is, top-left along the 45° diagonal (see Fig. 3, plots on the right). Accordingly, we tested whether the angle (\overline{biasHD}) was different from 45° . The results showed that in ROI17 and ROI18, the directions were not significantly different from 45° (p = 0.45 in ROI17, Cohen's d = -0.18 and p = 0.33 in ROI18, Cohen's d = -0.23), highlighting that the distributed activity in these two BA-areas coded for the specific direction of the target. By contrast, the direction of the (\overline{biasHD}) in ROI19 was significantly different from 45° (two-tailed one-sample t-test: $T(18) = -7.6$, p < 0.001 , Cohen's d = -1.75). The angle was smaller than 45° highlighting that, together with the selectivity for the target quadrant, the distributed activity in area BA19 also coded for an overall bias toward the hemifield containing the target. These effects can be seen in Fig. 5, plots on the right. In BA17 and BA18, the bias vectors for the HD condition (black) lie on the 45° diagonal (dotted line). In BA19, the HD vector also points to the top-left quadrant, highlighting the endogenous attentional bias towards the target quadrant. However, the BA19 vector's direction is offset from the diagonal (toward the y-axis) also indicating the presence of an overall bias toward the hemifield containing the target (i.e. the "IPSI" quadrant, corresponding to the other quadrant within the same hemifield where the target was presented).

Next we turned to our main question concerning the joint effects of endogenous and exogenous spatial attention in the occipital cortex. In order to assess the modulatory effect of exogenous attention on the spatial bias elicited by endogenous attention (cf. above), we tested for changes of the vector magnitudes and directions as a function of display-condition. Specifically, we tested for "Gains" related to salient target (STD vs. HD) and for "Costs" related to salient distractors (SDD vs. HD).

The results highlighted that salient targets lead to an increase of the magnitude of spatial bias coded in BA18 (one-tailed one-sample t-test, $T(18) = 4.2$, $p < 0.001$, Cohen's $d = 0.96$) and in BA19 ($T(18) = 4.4$, $p < 0.001$, Cohen's $d = 1$), while there was no significant magnitude gain in BA17 ($p = 0.71$, Cohen's $d = 0.09$). The vectors' directions were unaffected by the salient targets (i.e. no significant change of the vectors' angles; all p -values > 0.14 , all Cohen's d comprised between -0.06 and 0.35), including in BA19. The latter indicates that salient targets did not augment the spatial selectivity of the attentional bias in BA19. The comparison of the vectors in the SDD vs. HD display-conditions revealed that salient distractors reduced the magnitude of the bias in all 3 areas: BA17 ($T(18) = -3.8$, $p < 0.001$, Cohen's $d = -0.84$), BA18 ($T(18) = -4.0$, $p < 0.001$, Cohen's $d = -0.92$) and BA19 ($T(18) = -4.6$, $p < 0.001$, Cohen's $d = -1.06$). Again, the vectors' direction did not change significantly between HD and SDD (all p -values > 0.11 , all Cohen's d comprised between -0.19 and 0.09). Overall, the analyses of the bias vectors indicated that spatially-congruent exogenous signals boosted the spatial bias (salient targets), while incongruent signals reduced the bias (salient distractors). This was observed in all BA-areas, except for BA17 where the effect of salient targets was not significant. The analysis of the vectors' directions highlighted that distributed activity in BA19 coded for an overall bias towards the target hemifield and that exogenous signals did not modify this global effect of endogenous spatial attention.

We sought to establish the behavioral relevance of the spatial bias vectors by correlating the changes of the vector's magnitude (Gain_mag, Cost_mag) with the corresponding gains/costs at the behavioral level. Two separate multiple regressions analyses included reaction times differences (STD vs. HD, or SDD vs. HD) as the dependent variable and the Gain_mag (or Cost_mag) indexes of the 3 BA-areas as predictors. The Gain-regression yielded a non-significant model contribution compared to the "constant only" model (R -squared = 0.075 , $F(3,15) = 0.41$, $p = 0.75$), while the Cost-regression model highlighted a significant relationship between behavior and the imaging Cost_mag indexes (R -squared = 0.432 , $F(3,15) = 3.8$, $p = 0.033$). The regression coefficients highlighted the expected negative relationship between vector magnitude and RTs in BA18 (parameter estimate = -1.6 , $p = 0.018$), with more negative Cost_mag values (i.e. larger costs) associated with larger increases of reaction times (RTs_{SDD} vs. RTs_{HD}). By contrast the coefficient in BA17 was unexpectedly positive (parameter estimate = 1.19 , p

= 0.041) and the coefficient in BA19 was not significant (parameter estimate = 0.14, $p = 0.78$). Control multiple regression analyses that considered only activity in the ROI representing the target and the salient-distractor did not reach statistical significance for the relationship between brain activity and reaction times costs (ROI_IN: R-squared = 0.29, $F(3,15) = 2$, $p = 0.16$; ROI_OPP: R-squared = 0.34, $F(3,15) = 2.55$, $p = 0.09$).

2.3.4 Dynamic causal modeling (DCM)

A central aim of the current study was to investigate the mechanisms governing the generation of the attentional biases on the representation of visual space in the occipital cortex. Specifically, we evaluated the contribution of feed-forward/feedback connectivity between the occipital cortex and the dorsal attention control network, and of the lateral connectivity within the occipital cortex. In order to assess these different mechanisms, we constructed six dynamic causal models and used Bayesian Model Selection (BMS) to identify the model most likely to explain our data. Because our aim here was to test specific hypotheses about attentional biases in the occipital cortex, rather than exploring the full dynamics of all the brain areas engaging in the current task, the dynamic causal models included only 5 areas: the 4 occipital ROI18 providing us with a representation of the visual space and one area in the PPC belonging to the dorsal fronto-parietal attention network (BA7, ROI_PPC). The visual area BA18 was chosen based on the bias vector results (see above), and the PPC because it has been consistently considered a main source of the attention biases in the occipital cortex (e.g. Kastner, Pinsk, *et al.*, 1999; Vossel, Weidner, *et al.*, 2012, see also Discussion section). Each ROI was connected bi-directionally with all other ROIs and the models differed in terms of what connections could be modulated by the 12 attention conditions. The six dynamic causal models were organized into two families: the "diffuse PPC-BA18" family, where attention could modulate the connections between the ROI_PPC and all 4 ROI18; and the "focused PPC-BA18" family, where attention could modulate only the connections between the ROI_PPC and the occipital region representing the target quadrant (ROI18_IN). In each family, three DCMs embodied different patterns of attentional modulations between the occipital ROI18: modulation of all lateral connections, modulation of the connections from/to ROI18_IN only, or no modulation of the lateral connectivity (see Fig. 6, illustrating the whole DCM model space).

At the family level, BMS showed that the "diffuse PPC-BA18" family was most probable ($> 99\%$ posterior probability). This indicates that endogenous attention and visual salience most likely influence occipital activity via interactions between PPC and the full representation of the visual space coded by the 4 occipital ROIs, rather than selectively via modulation of the connectivity of the region representing the target quadrant (i.e. ROI18_IN, also cf. the bias vector results above).

At the model level, BMS showed that the dynamic causal model with the highest posterior probability included the modulation of the lateral connections between the ROI18_IN and the other 3 ROI18, in addition to the "diffuse" PPC-BA18 effects (see model in Fig. 6; > 99% posterior probability). Accordingly, endogenous spatial attention and visual salience operate not only by modulating top-down and bottom-up connectivity between the occipital cortex and the PPC, but also via the modulation of the lateral connectivity between the occipital region representing the attended quadrant (ROI18_IN) and the occipital regions representing the other parts of the visual field.

The choice of performing FFX-BMS rather than random effect (RFX) BMS was based on the fact that here the optimal model structure was expected to be the same across participants (K. Stephan *et al.*, 2010). However, for completeness, we also performed the complementary RFX-BMS, which confirmed our FFX-BMS results: at the family level the "diffuse PPC-BA18" family was the most probable (exceedance probability = 94%) and at the model level, the Model 2 (diffuse PPC-BA18, plus occipito-occipital connectivity involving ROI18_IN only) was again selected as the most probable model (exceedance probability = 45%, with the second best model at exceedance probability = 27%). This indicates that our FFX-BMS results were not due to outliers in our pool of participants.

Finally, we used Bayesian Parameter Averaging (BPA) to explore how the experimental conditions affected the different connections of the winning dynamic causal model. The connectivity parameters related to each ROI18 were averaged as a function of the target location and compared across the display-conditions (HD, STD and SDD). The results showed that salient targets (STD vs. HD) led to an increase of the bottom-up connectivity from the ROI18_IPSI to the ROI_PPC (posterior probability = 96.3%) and to a decrease of the connectivity between the ROI18_OPP and the ROI_PPC (posterior probability = 99.6%); see Fig. 7, on the left. The presentation of salient distractors (SDD vs. HD) lead to a more complex pattern of attentional modulations, affecting both the occipital-parietal connectivity and the lateral connectivity within BA18 (Fig. 7, on the right). Salient distractors lead to an increase of the top-down influence of the ROI_PPC on the target ROI_IN (posterior probability = 97.2%), as well as a decrease of the bottom-up signaling from the ROI_OPP (representing the salient distractor) to the ROI_PPC (posterior probability = 98.1%). This may correspond to a mechanism, mediated by the parietal cortex, seeking to maintain the processing priorities at the target location in spite of the salient distractor flashed in the opposite quadrant (see Discussion section). The analysis also showed that the presentation of the salient distractor yielded an increased lateral connectivity between the occipital ROIs. This included an augmented influence of ROI18_OPP to ROI18_IN (posterior probability = 99.7%), as well as a modulation of the connectivity between the ROI18_IN and the two ROIs representing

visual locations without any target or salient distractors (ROI18_IPSI, posterior probability = 98.0%; ROI18_CONTRA, posterior probability = 96.9%, see Discussion section).

In sum, the DCM analyses demonstrated that both changes of the occipito-parietal connectivity and changes of the lateral connectivity between the occipital regions that represent the different visual locations contribute to shaping the attentional bias in the visual cortex. The PPC was found to interact not only with the occipital region that represents the target location (ROI18_IN), but also with the regions representing unattended locations of the visual field. Together with these diffused interactions between the parietal and the occipital cortex, the DCM analyses revealed significant changes of the connectivity between the region representing the target and the other occipital regions, in particular when the visual display included a salient distractor.

2.4 DISCUSSION

We tested the joint influence of endogenous and exogenous spatial attention when participants were asked to judge a visual target presented among distractor stimuli. Our analyses focused on the modulation of activity in quadrant-specific occipital ROIs and on the effective connectivity between these areas and the PPC. We introduced a novel metric that, by using activity across regions representing different parts of the visual field, enabled us to index the direction and magnitude of the attentional bias in 2D space (spatial bias vectors) and we quantified the impact of endogenous and exogenous signals on this. The results revealed that both types of signals contribute to modulating the representation of 2D space in BA17, BA18 and BA19. Spatial endogenous attention was associated with a bias towards the target location and exogenous salience (color singletons) further modulated this spatial effect. Salience strengthened the spatial bias when the target was the color singleton, while it reduced the bias when a salient distractor was presented in the quadrant opposite to the target (Fig. 5). We found a significant correlation between these BOLD effects and the participants' reaction times, highlighting the behavioral relevance of the spatial bias vectors. The effective connectivity analyses revealed that the processing of salient signals involved both the modulation of lateral connectivity within the occipital cortex, as well as the bi-directional interactions between the occipital cortex and the PPC (Fig. 7). These findings demonstrate that the integration of endogenous and exogenous signals goes beyond the joint modulation of local activity, comprising instead the combination of bottom-up, top-down and lateral connections that governs competitive interactions and shapes the representation of space in the occipital visual cortex.

2.4.1 Endogenous spatial biases in the occipital cortex

A large body of previous work comprising both human neuroimaging and electrophysiology in non-human primates highlighted that endogenous spatial attention can modulate

visual processing in the occipital cortex (Heinze *et al.*, 1994; Desimone, 1998a; Reynolds, Chelazzi, *et al.*, 1999). Here, we used an independent localizer to map quadrant-specific ROIs in areas BA17, BA18 and BA19, and compared activity when endogenous attention was directed towards the location represented by the ROI (ROI_IN) versus activity in the opposite quadrant (ROI_OPP, i.e. the main effect of endogenous spatial attention). This showed that endogenous attention modulates occipital activity through the visual hierarchy, including quadrant-specific responses in anatomically-defined BA17, BA18 and BA19 (see Fig. 4). Of note, we found a robust modulation of activity in BA17 that corresponds to functional area V1. Attentional modulation in area V1 has been reported in several previous studies (e.g. Tootell *et al.*, 1998; Martínez *et al.*, 1999; Somers *et al.*, 1999), typically using displays containing dense arrays of stimuli (Brefczynski & DeYoe, 1999; Martínez *et al.*, 1999). Under these conditions, multiple items can fall inside the small receptive fields of V1 neurons and the attentional effects have been most often interpreted in the framework of the biased competition model (Desimone & Duncan, 1995; Kastner, Pinsk, *et al.*, 1999; Kastner, De Weerd, Pinsk, *et al.*, 2001; Bles *et al.*, 2006). By contrast, the visual display in the current study comprised simple and isolated stimuli that were located too far apart from each other to activate the same neuron in V1 (see also Gandhi *et al.*, 1999). Accordingly, mechanisms based on re-entrant feedback (Martínez *et al.*, 1999; Martin *et al.*, 2019), rather than the modulation of competitive interactions arising from feed-forward processing, are most likely to mediate the attentional effects in early visual areas that we observed in the present study, see also DCM results.

Besides highlighting the influence of endogenous attention in striate and extra-striate cortex, we characterized the spatial distribution of attention in 2D space. Previous studies demonstrated that spatial attention not only boosts responses in the occipital representation of the attended visual location (Kastner, Pinsk, *et al.*, 1999), but can also suppress activity associated with stimuli presented in other locations of the visual field (Smith *et al.*, 2000; Heinemann *et al.*, 2009). Thus, any comprehensive index of attentional selection should not rely only on changes of local activity. Several previous studies used multivariate approaches to characterize selective attention to visual categories (Reddy *et al.*, 2009) and, in the context of spatial attention, Melloni *et al.* (2012) proposed an index based on the numerical difference between activity in the occipital regions representing target vs. activity in regions that represent the distractor stimuli. The latter accounts for any suppressive effect at the non-attended locations, but averages activity in regions that may play different roles in spatial selection (e.g. representations of within- vs. between-hemifields locations; Scalf & Beck, 2010). The vector analysis that we propose here takes into account the level of activity in the four regions that represent other regions of visual field and provide us with both "strength" and "direction" information, as jointly coded by the four regions.

Considering the HD condition only (i.e. displays without any exogenous signal), the analysis of the vectors magnitude confirmed the effect of endogenous spatial attention in BA17, BA18 and BA19. The analysis of the vectors direction added to this that the bias in BA19 entailed a significant deviation from the target direction (cf. Fig. 5). Specifically, the attentional bias was directed towards the target quadrant, but also included an overall hemifield effect. The latter would be consistent with increased attentional priority for stimuli presented in the same hemifield as the cued-target, compared with stimuli in the opposite hemifield. Here we could not directly probe such hemifield advantage, because all the targets were presented at the cued location (i.e. 100% cue validity). Moreover, due to the short cue-to-target interval, we could not separate cue-related preparatory activity vs. attentional modulation of target-related activity. Assessing these effects would require several additional conditions (e.g. targets presented at uncued locations, within vs. between hemifields conditions) and longer cue-to-target intervals. This was not possible in the current study that aimed to investigate the spatial interactions between endogenous and exogenous attention and already comprised a large number of experimental conditions, see also Fig. S1A. However, this issue has been addressed in a recent electroencephalography study that used the same target discrimination task as here (Rashal *et al.*, 2022). Using both fully-predictive cues (as here) and no-cue trials, they showed that target selection (as captured by the "N2pc" component of the ERP) was observed in the no-cue condition, but not following fully-predictive cues. From these results, we suggest that the effects of endogenous attention we observed here (main effect of ROI-type/endogenous attention in Fig. 4) most likely reflects early attentional selection of the cued quadrant than later target selection processes.

Further, the use of a larger set of functional localizers (e.g. color, motion) and including retino-topic mapping for each participant would enable studying how the different functional areas belonging to the anatomically-defined BA19 (i.e. V3, hV4, V5) contribute to generating the deviation of the bias from the target location. The latter is a limitation of the current study that used only anatomical constraints to categorize functionally-defined quadrant-specific responses to different levels of the visual hierarchy (cf. Fig. 2A-B). Nonetheless, the current results in BA19 highlight the relevance of the spatial bias vectors in capturing the distribution of spatial attention in 2D space; see also below for additional findings linking the vectors' characteristics with behavioral performance.

2.4.2 Joint influence of endogenous attention and exogenous salience

The main objective of the study was to investigate how endogenous and exogenous spatial signals jointly contribute to modulating activity in the visual cortex. For this, the current experimental design manipulated orthogonally the endogenously attended

location (cued/target quadrant) and exogenous salience (display-condition). Standard analyses of local activity showed that visual salience led to quadrant-specific activation in all 3 BA-areas. The impact of salience was the same at the target location and at the distractor location, suggesting independent effects of the two types of control signals in the visual cortex (see also Sprague *et al.*, 2018). Importantly, it should be noticed that here salience was not confounded with luminance, as the latter was matched for salient and non-salient stimuli and the red/green color of the salient singleton was counterbalanced across participants (cf. Betz *et al.*, 2013 who reported contrast- rather than salience-dependent responses in V1-to-V3). The previous studies that assessed the interplay between endogenous attention and salience in the visual cortex provided us with mixed results (Melloni *et al.*, 2012; Sprague *et al.*, 2018; Won *et al.*, 2020, see also Hopf *et al.*, 2004, but using dense stimuli arrays). Melloni *et al.* (2012) reported a significant interaction between endogenous attention and the presence of salient distractors in area hV4, but not in areas V1, V2 and V3. By contrast, Sprague *et al.* (2018) reported significant effects of endogenous attention and stimulus salience throughout the visual hierarchy (V1, V2, V3A, hV4), but none of these areas showed a significant interaction (see also Poltoratski *et al.*, 2017). Finally, a recent study by Won and colleagues (2020) demonstrated that prior knowledge about the presence of distractors modulates the representation of salience in a single ROI that included areas V1, V2 and V3. Many different methodological aspects may explain these inconsistencies, including how endogenous attention was operationalized (blocked vs. mixed condition-order in Melloni *et al.*, 2012; fully-predictive central cues in Sprague *et al.*, 2018; distractor frequency in Won *et al.*, 2020), the manipulation of stimulus salience (color singletons in 4-items displays in Melloni *et al.*, 2012, 2012 and Won *et al.*, 2020); stimulus contrast in a 2-moving-items display in Sprague *et al.*, 2018) as well as the different analysis approaches (target minus distractor activity in Melloni *et al.*, 2012; reconstruction of spatial maps using an encoding model in Sprague *et al.*, 2018; MVP classification accuracy in Won *et al.*, 2020).

The one aspect likely to play a key role in determining the level of interaction between endogenous attention and salience concerns whether endogenous attention was fully focused at the target location or not, see also below. Melloni *et al.* (2012) and Won *et al.* (2020) employed search tasks entailing some uncertainty about the location of the target, while Sprague *et al.* (2018) and the current study used 100% valid spatial cues and thus endogenous attention was fully focused at the target location. The two studies that used search tasks (Melloni *et al.*, 2012; Won *et al.*, 2020) revealed significant interactions between endogenous attention and salience, both at the behavioral level and in the imaging data. By contrast, the behavioral data collected under fully-predictive cues did not demonstrate any significant effect of salience (here and in Sprague *et al.*, 2018), in agreement with previous behavioral studies indicating that endogenous control can abolish interference by salient distractors (e.g. Leber & Egeth, 2006; Leber, Gwinn,

et al., 2016; see also Luck, Gaspelin, *et al.*, 2021; see also Rashal *et al.*, 2022).

Nonetheless, at the imaging level both the current study and Sprague *et al.* (2018) found a robust activation of the visual cortex associated with the presentation of salient distractors. Further both studies computed spatial indexes in 2D space. Sprague *et al.* (2018) utilized an encoding model to reconstruct detailed 2D spatial maps indexing BOLD activity across the whole visual space, while here we used a simpler vector representation. Sprague *et al.* (2018) approach provides us with a detailed view of the representation of visual space, but the subsequent analyses relied on comparing activity in the reconstructed maps, without directly testing for possible changes in the geometrical characteristics of the 2D maps. By contrast, the spatial bias vectors used here comprise magnitude and direction information allowing us to assess separately the impact of salience on the strength of the attentional bias and its direction with respect to the target location. The analyses of vector magnitude demonstrated that salience modulated the spatial bias in all three BA-areas. In BA18 and BA19, we found that salient targets strengthened the attentional bias, while salient distractors reduced the bias. In BA17, the effect of singleton-distractors was also highly significant, but salient targets did not lead to any significant change of the bias magnitude compared with the no-salience condition (HD). The vector analyses did not reveal any significant change of the bias direction in any of the three BA-areas. However, it should be noticed that the salient distractors were always presented in the quadrant opposite to the target. This was done to restrict the total number of experimental conditions, but prevented us from testing the prediction that salient distractors in the contralateral - or the ipsilateral - quadrant would yield not only a reduction of the vector magnitude but also shifts of the vector direction. Nonetheless, additional analyses highlighted that the change of magnitude of the spatial vectors upon the presentation of salient distractors correlated with the corresponding reaction times costs, supporting the relevance of the 2D vectors' metrics.

These results, together with the robust response to salience in all tested visual areas, indicate that salient signals were not entirely suppressed despite the lack of any overall (mean) effects at the behavioral level. This adds to the long-lasting debate concerning the suppression of irrelevant salient distractors (Folk *et al.*, 1992; Theeuwes, 1994; Luck, Gaspelin, *et al.*, 2021). Specifically, there has been recent discussion about whether fully irrelevant salient items generate “attend-to-me” signals in the brain even though they do not imply behavioral costs (Geng, 2014; Geng & Duarte, 2021; Luck, Gaspelin, *et al.*, 2021). Sprague and colleagues (2018) found systematic salience signatures in the visual cortex without any behavioral gain (salient target) or cost (salient distractor), but did not provide any model of the suppression mechanisms that may explain the so-called discrepancy between brain-level and behavioral-level results. Here, we performed

analyses of effective connectivity that allowed us to study the fate of exogenous signals, as a function of whether they were presented at the endogenously attended (STD condition) or unattended (SDD) location, and we discuss this in relation to recent accounts of distractor suppression (Geng, 2014; Anderson, 2021; Geng & Duarte, 2021; Luck, Gaspelin, *et al.*, 2021), see next section.

2.4.3 Effective connectivity underlying the processing of salient signals in the visual cortex

Mechanisms of distractor processing have been most often associated with high-level regions in the frontal and parietal cortex (Melloni *et al.*, 2012; Suzuki & Gottlieb, 2013; Won *et al.*, 2020). The PPC is thought to play a central role, as the strength of its top-down influences on visual areas has been proposed to determine the fate of irrelevant distractors (Won *et al.*, 2020, and see Geng, 2014 for a review). Further, competitive interactions between relevant targets and irrelevant distractors can take place locally within the PPC, where priority maps would enable attentional selection by enhancing relevant signals and suppressing distractor signals at irrelevant locations (Gottlieb, 2007; Ptak, 2012; Geng, 2014; Zelinsky & Bisley, 2015; Bisley & Mirpour, 2019). Concurrently, competition at the level of the occipital sensory areas has been shown to contribute to attentional selection and distractor suppression (Luck, Chelazzi, *et al.*, 1997; Reynolds, Chelazzi, *et al.*, 1999; Reynolds & Desimone, 2003), leading to the proposal that also the occipital cortex comprises attentional priority maps (Mazer & Gallant, 2003, but see Betz *et al.*, 2013).

Here, we assessed the role of the occipital-parietal connectivity and of the lateral interactions within the occipital cortex using DCM (Friston, Harrison, *et al.*, 2003). We compared a set of models that differed in terms of how attention modulates these patterns of connectivity. The model space was designed with the aim to evaluate: 1) whether attention affects the occipital-parietal connectivity selectively for the target quadrant (ROI_IN), or it modulates also the connectivity between the parietal cortex and the other occipital ROIs; and 2) whether attention modulates the lateral connectivity between all the 4 occipital regions, the connectivity of the target-quadrant ROI only, or none of the lateral connections. In order to limit the number of nodes in the model, the DCM analysis considered only the 4 occipital ROIs belonging to BA18, where we found the most reliable correlation between the spatial vector magnitude and reaction times. Bayesian Model Selection (K. Stephan *et al.*, 2010) showed that the most likely model to explain the data comprised attentional modulation of all the occipital-parietal connections, plus the modulation of the lateral connectivity of the ROI_IN only.

These results indicate that multiple mechanisms can mediate the effect of attention on the representation of 2D space in the occipital cortex. Specifically, our activation data

demonstrated that endogenous attention and salience jointly modulate the representation of 2D visual space, beyond just affecting the activity of the regions that represent the target and the salient distractors (cf. above). The DCM results indicate that the spread of attentional effects across the different occipital regions can take place via multiple routes. First, the finding that attention modulates the connectivity between the PPC and all 4 visual ROIs provide us with an "indirect route" that would allow salient signals to be first transmitted to the PPC via feed-forward connectivity, and subsequently affect processing in all the visual areas via feed-back from PPC to the occipital cortex. In line with this, previous studies showed that attentional effects in the occipital cortex follow in time the activation of higher-level control regions in the parietal cortex (Martínez *et al.*, 1999; Martin *et al.*, 2019). Using high-temporal resolution intracranial electroencephalography, Martin *et al.* (2019) showed that after the initial feed-forward response to the stimulus-onset in the occipital cortex, spatially-specific modulatory feedback spread sequentially from parietal cortex back into the visual hierarchy, with increasing latencies from higher to lower areas (see also Lauritzen *et al.*, 2009). In the current study, convergent projections from the occipital regions that represent the different quadrants to the PPC would enable target and salient-distractors to interact, despite the large spatial separation between target and distractors. Feed-back connectivity from the PPC to the occipital cortex would then carry information about stimuli at far-apart locations, allowing such signals to affect activity also in visual areas that contain neurons with small receptive fields (e.g. BA17/V1 and BA18/V2).

Consistent with a role of PPC in the processing of salient distractors, Bayesian parameter averaging that tested for attention-related changes of effective connectivity revealed both a reduction of the feed-forward connectivity between the visual region activated by the salient distractor (ROI_OPP) and an increase of the parietal feed-back on the occipital region representing the target (ROI_IN; cf. Fig. 7, panel on the right). The strengthened top-down effect is consistent with the mechanism described above and may reflect the "choice" of the currently relevant location, following competitive interactions between endogenous attention and salience at the level of the parietal cortex. Concurrently, the reduction of feed-forward connectivity from ROI_OPP to the PPC suggests that attention can counteract the augmented occipital activity generated by the salient distractors. Specifically, unlike previous studies reporting that endogenous attention results in a suppression of activity at unattended locations (Smith *et al.*, 2000; Heinemann *et al.*, 2009), here we found no reduction of salient-distractors activity (cf. main effect of salience, Fig. 4). Instead, the DCM results showed a decrease in the efficiency with which these signals propagate from the occipital to the parietal cortex. The latter may constitute an additional mechanism that reduces the impact of salient irrelevant stimuli on any parietal mechanism that integrates attentional signals at the local level (cf. priority maps Gottlieb, 2007; Ptak, 2012; Zelinsky & Bisley, 2015; Bisley

& Mirpour, 2019). These results come in support of theoretical views that attentional priority processing emerges from computations taking place in different brain areas (Corbetta & Shulman, 2002; Vossel, Weidner, *et al.*, 2012; Vossel, Geng, *et al.*, 2014; Geng, 2014; Anderson, 2021). In other words, the presence of the neural signature of an irrelevant salient item does not imply that the output behavioral response will be substantially affected by this item: other regions of the fronto-parietal attentional network (here the PPC) can suppress the bottom-up signal generated by the irrelevant salient item so that attentional priority is reorganized and focused on the target item (Geng, 2014; Anderson, 2021; Geng & Duarte, 2021).

It should be noticed that our DCM analyses included a single node belonging to the fronto-parietal attention control networks (i.e. the ROI_PPC). The reason for this was that our hypotheses targeted the role of lateral connectivity within occipital cortex vs. the connectivity between these quadrant-specific regions and higher-order regions. The choice of the PPC was dictated by extensive evidence pointing to this region as the source of attentional modulation on the visual cortex (e.g. Buchel, 1997; Vossel, Weidner, *et al.*, 2012, see also Desseilles *et al.*, 2011 for modulation of V1). Nonetheless, it should be acknowledged that many other areas - and paths - are likely to be involved in the current task. These include dorsal premotor regions that have been found to exert top-down influences on the occipital cortex (Buchel, 1997; Melloni *et al.*, 2012, and see Moore & Armstrong, 2003 for single-cell electrophysiology) and that, together with the PPC, contribute to the integration of bottom-up and top-down signals for visuo-spatial attention control (Brázdil *et al.*, 2007; Buschman & Miller, 2007; Ibos *et al.*, 2013; Suzuki & Gottlieb, 2013; Bowling *et al.*, 2020). In addition, the PPC is often identified as a spatially-specific map of the environment responding to both goals and salience (Gottlieb, 2007; Ptak, 2012, see also spatial mapping of the PPC, Silver & Kastner, 2009; Mackey *et al.*, 2017) and has been shown to respond bilaterally to salient distractors (Won *et al.*, 2020). However, there is also evidence supporting that the left and right PPC are associated with different aspects of salience processing. Using transcranial magnetic stimulation, Mevorach *et al.* (2006) and Hodsoll *et al.* (2009) showed that the right PPC was associated with the selection of salient stimuli, while left PPC was associated with the ability to ignore salient stimuli. Accordingly, future work should seek to examine the spatial specificity of target/distractor effects - at the same time - in the occipital cortex and in the posterior parietal cortex (plus possibly other regions of the dorsal fronto-parietal network, e.g. FEF: frontal eye-field). This would help to better understand the relationship between mechanisms of spatial attention in the occipital cortex (as in the present study, and see also Melloni *et al.*, 2012; Sprague *et al.*, 2018; Won *et al.*, 2020) and in hierarchically higher areas related to attentional control. Moreover, our model did not include any node belonging to the ventral attention system (TPJ: temporal-parietal junction, and IFG: inferior frontal gyrus). These regions

are typically associated with re-orienting towards salient task-relevant stimuli (Corbetta, Kincade, *et al.*, 2000) or irrelevant stimuli that share some feature with the target (Natale, C. Marzi, *et al.*, 2010). Dorsal and ventral fronto-parietal regions are thought to work together during visuo-spatial attention control (Corbetta & Shulman, 2002; Corbetta, Patel, *et al.*, 2008; Vossel, Weidner, *et al.*, 2012; DiQuattro, Sawaki, *et al.*, 2014) and, most likely, participated to the current attention task together with the PPC.

Most important here, our DCM results showed that beside any interaction between the occipital cortex and higher-order fronto-parietal regions, attention modulated the effective connectivity within the occipital cortex. The winning model included modulation of the connections of only the region representing the current target location (ROI_IN). As noted above, the role of attention in modulating competitive interactions in the visual cortex is well understood in the framework of the biased competition model (Desimone & Duncan, 1995; Beck & Kastner, 2005; Yantis, 2005), but such interactions require target and distractor stimuli to fall within the receptive field of the same neuron. This was most likely not the case for area BA18 in the current study, which included stimuli presented at a distance of 10° and across the visual quadrants. One previous study directly addressed the influence of attention on the pattern of connectivity between occipital regions representing locations further apart in the visual field (Haynes *et al.*, 2005). The study targeted the integration of information across distant locations, when attention was divided between two quadrants while the other two quadrants contained unattended distractors. The analyses of effective connectivity considered the 4 ROIs representing the 4 quadrants, in V1, V2 and V4. Attention was found to modulate the connectivity between the different levels of the visual hierarchy (feed-forward and feed-back), as well as to increase the lateral connectivity between the 2 ROIs representing the two attended quadrants within the same area.

Unlike this previous study, here the attention task implied selecting the stimulus at the target location, while ignoring the stimuli in all the other quadrants. Bayesian parameter averaging that tested for changes of lateral connectivity in the salient distractor condition (SDD vs. HD, see Fig. 7, right panel) showed that the color-singleton augmented the influence of the ROI_OPP (i.e. the region receiving the salient input) on the target-quadrant ROI_IN, as well as the outgoing connectivity from ROI_IN to both ROI_CONTRA and ROI_IPSI. We propose that these effects reflect fast exogenous influences signaling the presence of salient stimulus (see also Martin *et al.*, 2019, reporting fast attentional effects in the early visual cortex that are inconsistent with parietal feed-back mechanisms). Here the spreading of salience-related signals through all the occipital regions, including the ROIs representing locations contralateral and ipsilateral to the target location (ROI_CONTRA and ROI_IPSI), seems consistent with the results of the bias vector analysis showing that, in terms of correlation with

reaction times, the impact of salient distractors correlated with the bias vectors computed using the combined activity of the 4 occipital ROIs (cf. above). Also, the finding of significant changes between the ROI_IN and both CONTRA and IPSI ROIs fits with the observation that salient distractors impacted on the vector's amplitude but not on direction. Indeed, any differential effect over the two ROIs - with the resulting unbalance of the local activities - would result in a shift of the bias vector direction towards the quadrant represented by the most active ROI.

In the framework of DCM analyses, it is important to stress that the attentional modulation of the lateral occipital-to-occipital connectivity does not imply the existence of any direct, mono-synaptic anatomical connection between the occipital ROIs. Instead, signaling via sub-cortical regions (Martin *et al.*, 2019) and/or reentrant circuits involving higher-order areas (Haynes *et al.*, 2005; Turova & Rolls, 2019) may mediate the observed changes of effective connectivity. Furthermore, it should be noted that here we compared a restricted set of DCM models, but a large number of alternative models could also be tested by combining the presence or absence of specific intrinsic connections (A-parameters, which were not manipulated here) and/or more specific combinations of the modulatory effect of the experimental conditions (B-parameters). Nonetheless, the current finding that intra-occipital connectivity operates in addition to any interactions between the occipital and the parietal cortex supports the notion that attentional selection should be understood in terms of distributed representations of space, rather than just the modulatory influence that the fronto-parietal control network exerts on the visual cortex. Future studies could address this further, for example, by interfering (e.g. via transcranial magnetic stimulation) with attentional control via stimulation of occipital regions that represent spatial locations other than those containing the target or the salient distractor. Based on the current results, we anticipate that this would contribute to biasing the 2D representation of space within the occipital cortex, also affecting the processing of target/distractors presented at different locations in the visual field.

2.5 CONCLUSIONS

We investigated how endogenous spatial attention and stimulus salience contribute to quadrant-specific activations in the occipital cortex. We quantified the impact of attention on the representation of visual space by using a vectorial index that provided us with both magnitude and direction of the attentional bias in 2D space. We found significant effects of endogenous spatial attention in anatomically-defined BA17, BA18 and BA19, including an overall hemifield bias in BA19. Salient target-singletons enhanced the attentional bias magnitude, while salient distractors reduced it. The latter was found to correlate with the corresponding reaction times costs. Analyses of effective connectivity revealed that both occipito-parietal connectivity and lateral influences within the occipital cortex explain

these distributed attentional effects. These findings demonstrate that endogenous and exogenous attention jointly contribute to shaping processing priorities in the occipital cortex and highlight that multiple functional paths determine how information about these two types of signals is distributed across the different regions that represent visual space.

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2.6 SUPPLEMENTARY MATERIAL

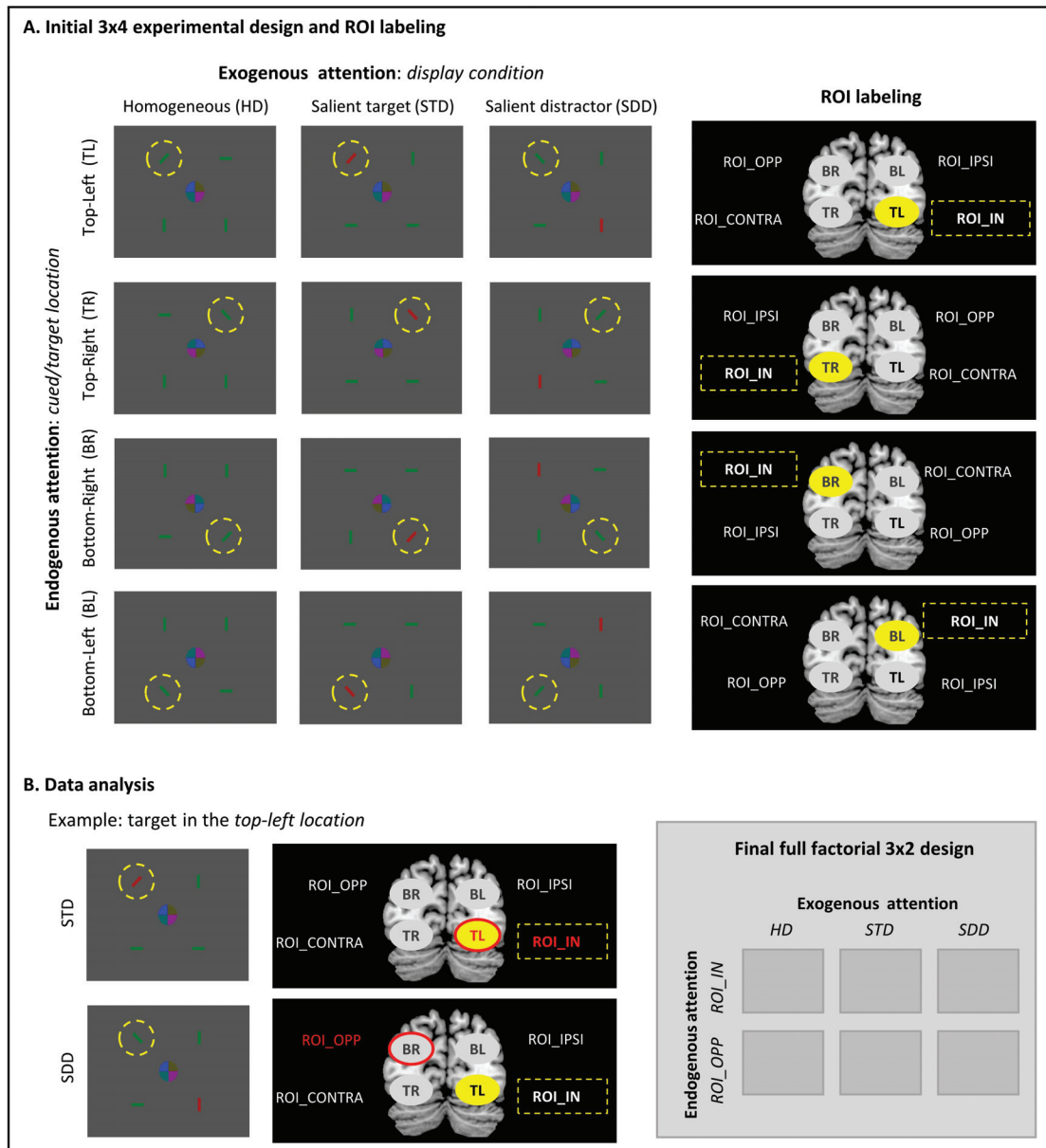


Figure 2.8: **Figure S1. Relationship between experimental design, ROI labeling and univariate data analysis.**

A - The 12 experimental conditions organized according to a 3 x 4 full factorial design. The two orthogonal factors correspond to exogenous attention (3 levels of display-condition: no salient items [HD, homogeneous display], salient target display [STD] and salient distractor display [SDD]) and the endogenously attended position (4 levels: top-left [TL], top-right [TR], bottom-right [BR], bottom-left [BL]). On the left panels, the dotted yellow circle indicates the endogenously attended location that was cued at the start of each trial using a composite central symbolic cue (here, the relevant cue-color is blue) and that always contained the target item (tilted bar, 100% cue validity). The panels on the right illustrate the labeling of the occipital ROIs, as a function of the endogenously attended location. The yellow ellipses show the ROIs that represent the endogenously attended quadrant and are labeled “ROI_IN”. The same procedure applies to the other quadrant-representations and yields to the labels: ROI_OPP for the occipital regions representing the quadrant opposite to the target position, ROI_CONTRA for the regions representing the quadrant contralateral to the target and ROI_IPSI for the regions representing the quadrant in the same hemifield as the target. This procedure was applied to individually-defined ROIs located in Brodmann’s area BA17, BA18 and BA19 (see Fig. 2). **B** - Final 3 x 2 full factorial design used for the univariate data analysis. The univariate data analysis averaged the parameters estimates of the general linear model (see Methods section) considering the relationship between the quadrant represented by each ROI and the current direction of endogenous spatial attention. Specifically, we considered activity in the ROIs representing the target location (ROI_IN) and the opposite quadrant (ROI_OPP), where salient distractors were presented in the SDD condition (see panel on the left for an example). Formally this resulted in a 3 x 2 full factorial design, comprising the two orthogonal factors of exogenous attention (again, the 3 display-conditions) and endogenous attention, now operationalized as the activity in the ROIs representing the endogenously attended quadrant (ROI_IN) vs. the ROIs representing the opposite quadrant (ROI_OPP). The panel on the left illustrates an example of the manipulation of endogenous attention (represented in yellow) and exogenous attention (highlighted in red). In the STD condition, the ROI_IN activity comprises both endogenous and exogenous effects. In the SDD condition, the ROI_IN activity is related to endogenous attention while the ROI_OPP activity is related to exogenous attention (salience). The left panel summarizes schematically the two factors and the 6 cells of the final 3 x 2 factorial design.

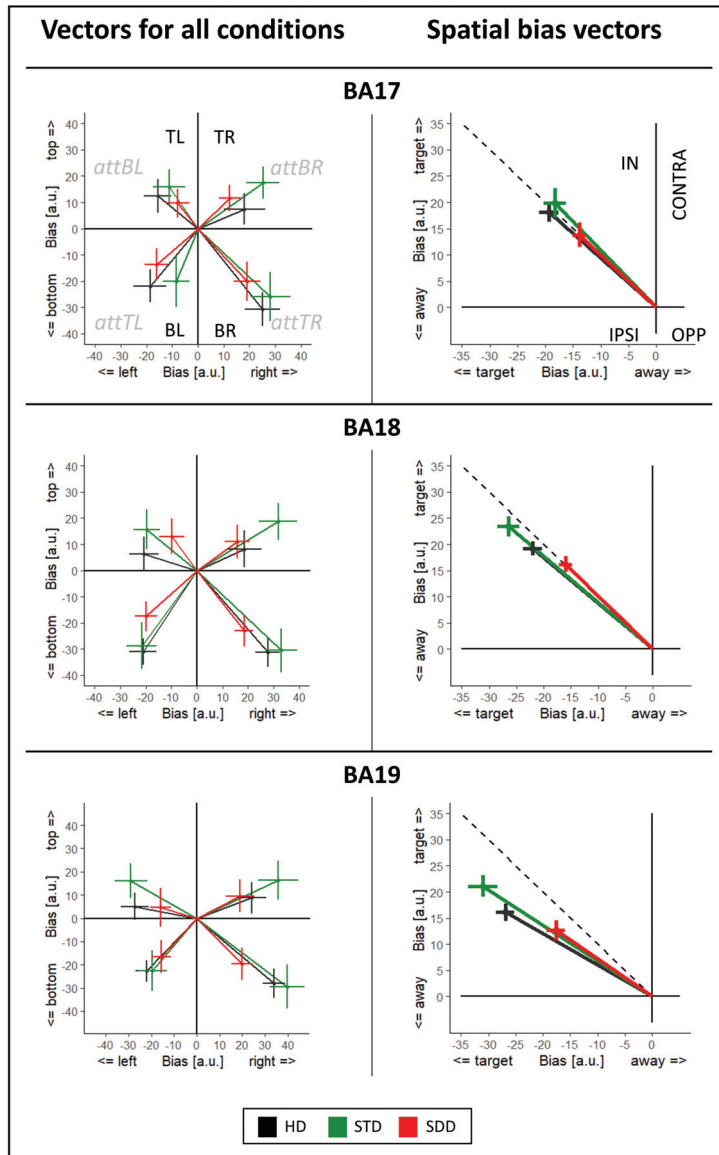


Figure 2.5: **Figure 5. Spatial biases elicited by endogenous and exogenous attention.**

The plots on the left show the condition-specific 2D vectors plotted separately for the four attended quadrants (*attTL*, *attTR*, *attBR*, *attBL*) and display-condition (HD, STD, SDD). In all 3 display-conditions, the bias vectors were directed towards the target quadrant, reflecting the main effect of endogenous attention. The plots on the right show the final spatial bias vectors comprising the magnitude and the direction of the attentional effects in the three BA-areas, as a function of display-condition. The analysis of the vector-magnitudes showed that salient distractors reduced the spatial bias in all BA-areas (compare SDD-red vs. HD-black vectors) and that salient targets strengthened the bias in BA18 and BA19 (STD-green vs. HD-black). The vector-direction analysis highlighted that in BA19 attention also triggered an overall bias towards the target hemifield (in the rightmost plot, compare the direction of the bias vectors with the dotted-line that indicates the direction of the target). This was unaffected by the display-condition. Please note that in these plots the IPSI/CONTRA labels refer to the location of the target, not to some anatomical location in the brain. Crosses represent standard errors of the mean of the horizontal and vertical coordinates. L/R: left/right; T/B: top/bottom. OPP/CONTRA/IPSI: opposite/contralateral /ipsilateral with respect to the target quadrant (IN).

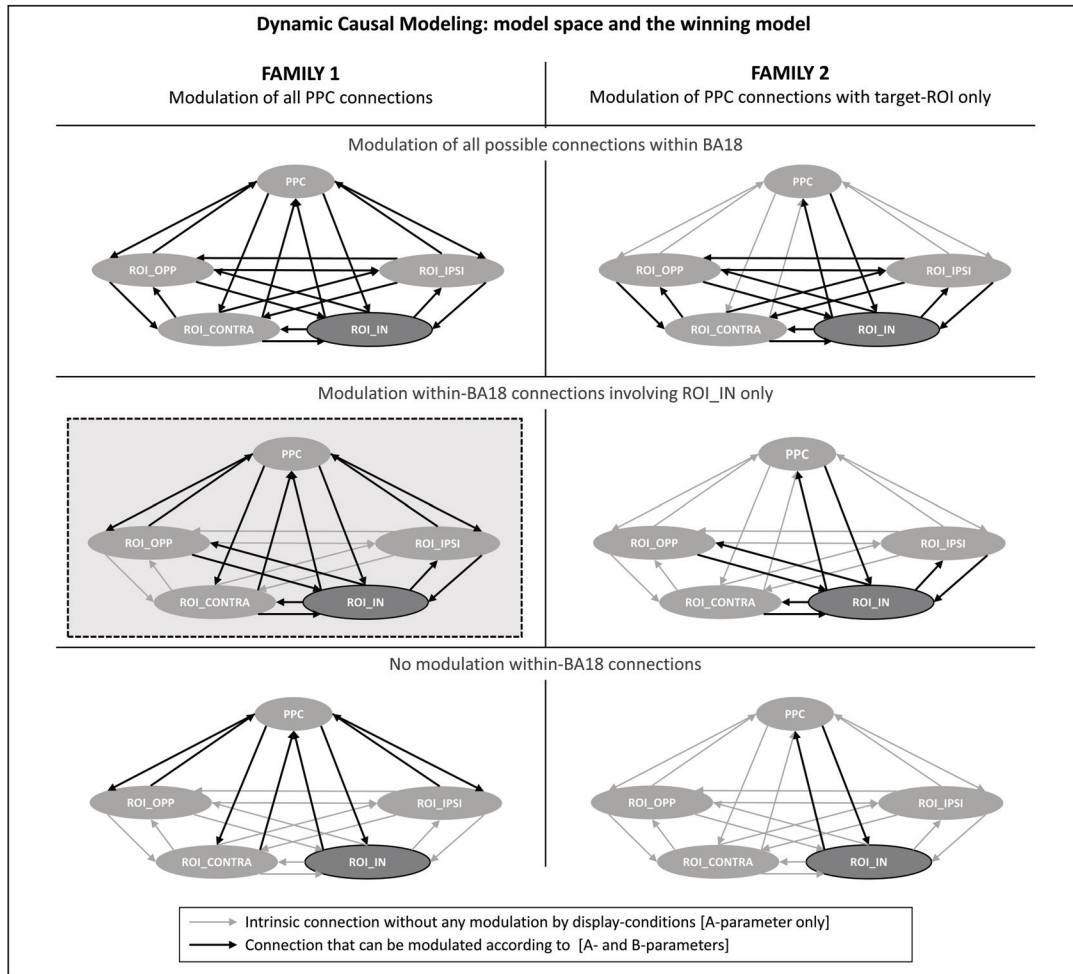


Figure 2.6: **Figure 6. Dynamic Causal Modeling: model space and the winning model.**

The model space served to test hypotheses concerning the attentional modulation of the connectivity between the posterior parietal cortex (PPC) and the four regions in BA18 that represent the visual field. All models comprised the same set of intrinsic connections [A-parameters] that reciprocally linked all 5 nodes. The models differed in terms of the connections that could be further modulated according to the 3 display-conditions [B-parameters]. The 6 models were partitioned in two families: Family 1 considers diffused interactions between PPC and all the occipital BA18 regions, while Family 2 considers that attention modulates only the connectivity between PPC and the occipital region that represent the target location (ROI_IN). In each family, 3 different models account for different patterns of effective connectivity within BA18: one model includes modulation of all connections between the 4 BA18 ROIs; the second model includes only the modulation of the connections involving the region that represents the target (ROI_IN); the third model does not allow for any attentional modulation of the intra-areal connectivity between the 4 BA18 ROIs. Black arrows highlight what connections can be modulated by the display-conditions, grey arrows represent connections that cannot be modulated by attention. Bayesian Model Selection revealed that the model most likely to explain the data included modulation of all the connections between PPC and BA18 and within-BA18 connectivity including only the region that represent the current target location (family 1, model 2: highlighted with dotted-line). PPC: Posterior parietal cortex; ROI_ OPP/CONTRA/IPSII: ROIs opposite/contralateral/ipsilateral with respect to the ROI representing the target quadrant (ROI_IN).

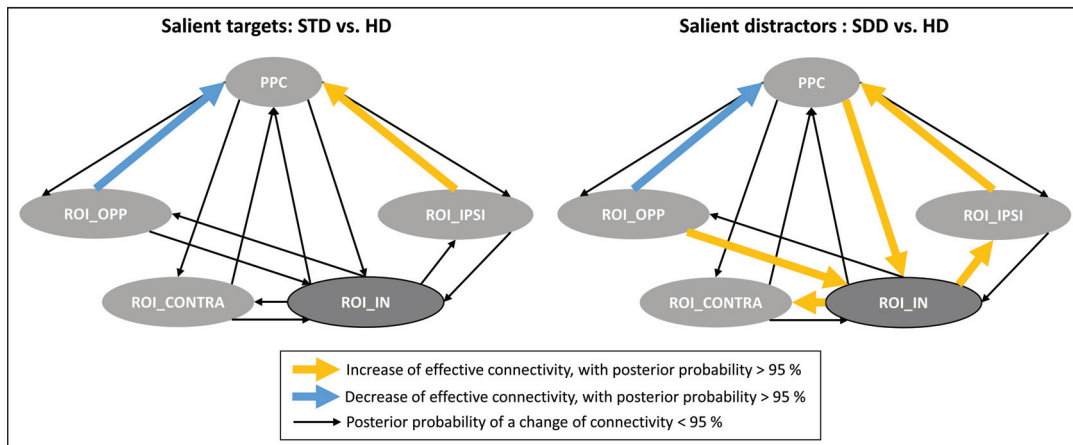


Figure 2.7: **Figure 7. Dynamic Causal Modeling: connectivity parameters of the winning model.**

The winning model included diffused interactions between PPC and all the occipital BA18 regions. Bayesian Parameter Averaging of the winning model tested for the effect of “salient targets” (STD vs. HD, shown on the left) and the effect of “salient distractors” (SDD vs. HD, shown on the right). For each comparison, the thick-colored arrows highlight changes of connection strength with posterior probabilities equal or larger than 95%. ROI_OPP/CONTRA/IPSI: ROIs opposite/contralateral/ipsilateral with respect to the ROI representing the target quadrant (ROI_IN). Please note that the figure shows only the connections of the winning model that could be modulated by the experimental conditions [B-parameters], while the intrinsic connections that linked all 5 nodes of the model [A-parameters] are not shown here (cf., winning model highlighted in Fig. 6).

Brodmann Area	ROI	Mean number of voxels \pm SEM
BA17		
	ROI17_TL	75.37 \pm 11.25
	ROI17_TR	90.68 \pm 12.04
	ROI17_BR	105.21 \pm 15.37
	ROI17_BL	57.68 \pm 6.13
BA18		
	ROI18_TL	160.42 \pm 16.10
	ROI18_TR	208.79 \pm 16.31
	ROI18_BR	293.63 \pm 26.53
	ROI18_BL	217.26 \pm 19.59
BA19		
	ROI19_TL	168.84 \pm 17.15
	ROI19_TR	177.26 \pm 17.17
	ROI19_BR	174.53 \pm 21.96
	ROI19_BL	231.05 \pm 25.36
BA7		
	ROI_PPC	2029.40 \pm 106.47

Figure 2.9: Table S1. Mean size (in voxels) \pm SEM of the occipital (BA17, BA18, BA19) and parietal (BA7) Regions of Interest.

Chapter 3

Experiment 2 - Separate and overlapping mechanisms of statistical regularities and salience processing in the occipital cortex and dorsal fronto-parietal regions

Manuscript in preparation

ABSTRACT

Attention selects behaviorally relevant inputs for further in-depth processing. Beside the role of traditional signals related to goal-directed and stimulus-driven control, it exists a debate regarding the mechanisms governing the effect of statistical regularities on attentional selection. Here, we tested the joint effects of statistical regularities and stimulus-driven salience on the brain correlates of visuo-spatial attention. We found that both statistical regularities and salience modulated occipital activity in a spatially-specific manner, but also that these effects changed along the different levels of the visual hierarchy. In addition, we found that both statistical learning and salience activated the dorsal frontoparietal network, but analyses of functional connectivity revealed that only statistical learning modulated the inter-regional coupling between the posterior parietal cortex and the occipital areas. The latter suggests that salience relies primarily on local interactions within the occipital cortex, while statistical regularities processing also requires a parietal-occipital interplay. Together, these results show that statistical regularities and salience signals are both spatially represented at the occipital level, but that their integration into attentional processing priorities rely on different brain mechanisms.

3.1 INTRODUCTION

Visual selective attention (VSA) is a cognitive function that allows to prioritize behaviorally relevant information among the large amount of visual information that competes for cognitive processing (Clark, 2003; Dukas, 2004; Chelazzi, Della Libera, *et al.*, 2011). Traditionally, the factors accounting for the behavioral relevance of visual items or portions of the visual field – also called “attentional priority signals” – have been classified in two categories: endogenous and exogenous signals. Endogenous signals generally refer to information related to the current goals of the participant, while exogenous, stimulus-driven signals guide selection on the basis of low-level physical features of the sensory input (e.g.: color, motion or orientation contrasts, Itti & Koch, 2001; Desimone & Duncan, 1995; Egeth & Yantis, 1997). This dichotomy has been linked to separate functional networks in the frontal parietal areas that are ought to guide attention on the basis of endogenous (dorsal network) or exogenous signals (ventral network, Corbetta, Kincade, *et al.*, 2000; Corbetta & Shulman, 2002; Chica, Bartolomeo & Valero-Cabre, 2011). Nonetheless, this traditional account has been recently challenged.

First, a strong dichotomy between endogenous and exogenous control does not seem to best account for the attentional control requirements of any real-life condition, where visual scenes most of the time contain complex combinations of stimulus-related exogenous signals and task-relevance (Koch & Ullman, 1985; Itti & Koch, 2001; Thompson & Bichot, 2005; Chelazzi, Della Libera, *et al.*, 2011; Macaluso & Doricchi, 2013). This issue has been increasingly addressed, indicating that the joint contributions of endogenous and exogenous priority signals on behavioral performance depends on the task configuration. In classical visual search tasks, the task-relevant target can be more easily found when it is also the (exogenously) salient item, while it is harder to find when it is presented together with a salient distractor (Desimone & Duncan, 1995; Melloni *et al.*, 2012). However, when the target defining-feature/location is (endogenously) cued before the stimulus array is presented, then the salience-driven priority of the target - or of the distractor - is suppressed, leading to little facilitation/impairment at the behavioral level (Sprague *et al.*, 2018; Beffara *et al.*, 2022, and see Geng, 2014; Anderson, 2021; Geng & Duarte, 2021; Luck, Gaspelin, *et al.*, 2021 for reviews about distractor suppression). These behavioral findings suggest that endogenous and exogenous signals are not processed by fully independent cognitive systems but rather work together to jointly affect the allocation of attentional resources, leading to different behavioral outcomes depending on the relative weights of these signals.

Second, the traditional dichotomy between endogenous and exogenous control was put forward within a framework where endogenous control was strongly associated with intentional, goal-directed attention (Corbetta & Shulman, 2002; Awh *et al.*, 2012). However, there is now extensive evidence that other types of priority signals can also

contribute to VSA, including emotional content (Vuilleumier, 2005; Todd & Manaligod, 2018), semantics (e.g. Gibson & Kingstone, 2006), reward (Pessoa, 2010; Anderson, Laurent, *et al.*, 2011; Awh *et al.*, 2012; Chelazzi, Perlato, *et al.*, 2013; Chelazzi, Estocinova, *et al.*, 2014; Anderson, 2016; Bourgeois, Chelazzi, *et al.*, 2016) and social factors (Klein *et al.*, 2009). An additional category of attention priority signals concerns the selection history/statistical learning (Awh *et al.*, 2012). This refers to any recurring pattern (statistical regularities) of sensory information that can bias attentional selection regardless of the current items' salience and participants' goals (Awh *et al.*, 2012). During visual search tasks, selection history acts by behaviorally facilitating search when the uncertainty due to the task configuration is limited (e.g. when the features of the to-be-detected target are known).

At the behavioral level, Wolfe and colleagues (2003) compared response times (RT) to identify a target whose defining-features were either kept constant (e.g. the target was always the red among green items) or mixed within an experimental block (e.g. the target could either be the red among green items, or the vertical among horizontal items). The results showed slower RT when uncertainty was high (mixed target defining-feature within an experimental block) than when it was low (varying target defining-feature within an experimental block). Although these findings were initially interpreted as being due to a difference of the engagement of endogenous, goal-directed attention between the 2 experimental conditions (Wolfe *et al.*, 2003), Awh and colleagues (2012) proposed another interpretation considering that the difference of endogenous engagement may be confounded with the priming of the current target by previous targets. Indeed, in the fixed/constant target blocks, successive trials always comprised targets with the same defining-feature. Similarly, Melloni and colleagues (2012) aimed at investigating the mechanisms of distractor suppression and target enhancement when trial-types could or not be anticipated across trials. They compared experimental runs comprising mixed trial-types (trials in these runs could either comprise items all of the same color [homogeneous displays, HD], or the target was a salient color singleton [salient target display, STD], or one of the distractors was the color singleton [salient distractor display, SDD]) with runs comprising the very the same trial-types but now presented in a blocked manner. Comparably to the results in Wolfe and colleagues (2003), they found poorer behavioral performances in mixed compared to blocked runs. Together, these findings show that target selection can be facilitated, or impaired, depending on the participants' knowledge regarding the probabilistic structure of the search conditions across trials (i.e. the trial history).

While these studies investigated the impact of trial history on behavioral performance, they did not assess how attentional priority is attributed to a specific spatial location, as a function of selection history in the spatial domain. Addressing this issue is crucial

to dissociate any attentional gain related to spatial expectations (e.g. recurrent target or distractor location) vs. current goals (current target location) and physical salience (see “priority maps framework”, Gottlieb, 2007; Awh *et al.*, 2012; Ptak, 2012; Bisley & Mirpour, 2019). With this aim, a behavioral study by Ferrante and colleagues (2018) tested the joint contribution of selection history and physical salience to target selection. They used a search task comprising spatially-specific probabilities of target and salient distractor location. There were 2 display-conditions and 3 probabilistic contexts. In one display-condition all 4 items were of the same color (HD condition, cf. Melloni *et al.*, 2012 above), while in the second condition one of the 3 non-targets was a color singleton (SDD condition). These two types of search arrays were tested when the target was presented at a high (HTPL), intermediate (ITPL) or low (LTPL) target-probability location. The results showed a significant main effect of the display-condition, with poorer performances in SDD than in HD, as well as a significant main effect of target location, with better performances when the target was at HTPL compared to ITPL and poorer performances when target was at LTPL compared to ITPL. The interaction between the 2 factors was also significant, with a stronger effect of target location in SDD compared to HD. These findings demonstrate that statistical regularities and physical salience can jointly contribute to target spatial selection. In addition, when a salient distractor was presented at the HTPL location (SDD), the behavioral performance was poorer than when it was presented at the ITPL or at the LTPL (Ferrante *et al.*, 2018), suggesting that priorities can be attributed across space rather than across features: expectations can shape the attentional gain attributed to specific spatial locations independently of the type of item (target or distractor singleton) presented at those locations.

At the brain level, recent models of attention control posit that attentional gains are attributed to each specific spatial location of the visual display represented in so-called “spatial priority maps” that would combine different types of control signals (Thompson & Bichot, 2005; Gottlieb, 2007; Ptak, 2012; Bisley & Mirpour, 2019). Priority maps have been associated with regions of the dorsal fronto-parietal attention network (intraparietal sulcus, IPS; frontal eye field, FEF; Thompson & Bichot, 2005; Gottlieb, 2007; Ptak, 2012; Bisley & Mirpour, 2019), as well as sub-cortical structures such as the superior colliculus (Bisley & Mirpour, 2019). In addition, several human fMRI studies that specifically addressed the role of selection history in attentional selection highlighted the possible contribution of spatially-specific maps of the occipital visual cortex to the definition of attentional priorities (Melloni *et al.*, 2012; Won *et al.*, 2020; Zhang *et al.*, 2021).

Melloni and colleagues (2012) showed that when participants could predict the configuration of the search array, the differential activity between the occipital regions (V2 and V4) representing the target location and the occipital regions representing the

distractor location was larger than when the participants ignored what would be the upcoming display configuration (blocked- vs. mixed-trials, cf. above). The whole-brain analyses revealed also activation of the IPS in the dorsal fronto-parietal network, when comparing "SDD-blocked minus SDD-mixed" versus "HD-blocked minus HD-mixed". The latter interaction between predictability and salience suggests that the IPS mediates proactive distractor processing, when the participants can anticipate the upcoming display configuration. In a more recent study, Won and colleagues (2020) extended the work of Melloni and colleagues (2012) by testing more specifically how expectations about the display configuration modulate activity in occipital regions representing the target and the distractors. In Won and colleagues (2020), the participants were now informed about the (high/low) likelihood that the search array would contain a salient distractor. The results showed that the activity of the occipital region representing the salient distractor location was reduced when participants expected the presentation of the salient distractor compared with the low expectation condition, which had not been directly assessed in Melloni and colleagues (2012). This suggests that the expectation of a salient distractor in the upcoming trial can counteract any activation associated with the distractor's salience and, thus, that expectations can facilitate distractors' suppression. Nonetheless, at odds with whole-brain results in Melloni and colleagues (2012), Won and colleagues (2020) found larger activation of the IPS for salient distractors presented under low versus high expectation conditions. Won and colleagues (2020) suggested that regions of the frontoparietal networks were not recruited for proactive distractor suppression (under high distractor singleton expectations), which instead would occur automatically within the occipital cortex, provided that distractor suppression occurs in an efficient manner (see also Geng & Duarte, 2021, for review).

In another recent study, Zhang and colleagues (2021) manipulated the probability for a salient distractor to be presented in a specific spatial location unbeknownst to the participants, hence addressing more specifically expectations about spatial locations (cf. Ferrante *et al.*, 2018, above). In line with the two previous studies, the results showed that irrelevant salient distractors presented at the expected location elicited weaker responses in the corresponding occipital representation, compared with the salient distractors presented at a low probability location. Also, consistent with Won and colleagues (2020), whole-brain analyses revealed greater activation of the superior parietal lobule (SPL) when the salient distractor was at a low compared to a high probability location. Altogether, these results show that expectations about the presence/location of task-irrelevant distractors modulate spatially-specific responses in the occipital visual cortex (Melloni *et al.*, 2012; Won *et al.*, 2020; Zhang *et al.*, 2021). This modulatory effect co-occurs with the deactivation of dorsal parietal regions (SPL /IPS) that may mediate distractor suppression when the participant can anticipate the presence and/or location a salient distractor in the upcoming search trials (Geng, 2014; Won *et al.*, 2020; Geng &

Duarte, 2021; Zhang *et al.*, 2021).

The priority maps framework would predict that statistical regularities should enhance spatial representations of task-relevant target location (e.g. in the occipital cortex) and suppress the location of expected task-irrelevant distractors (see discussion in Zhang *et al.*, 2021 and see behavioral results in Ferrante *et al.*, 2018). Although this specific prediction has never been formally tested using spatial attention protocols, statistical regularities related to task-relevant targets have been previously associated - somewhat counterintuitively - with so-called “expectation suppression” rather than enhancement (Richter & de Lange, 2019; Alink & Blank, 2021). In particular, Richter & De Lange (2019) used fMRI to investigate the non-spatial responses to predicted/expected stimuli. In a training phase, on each trial a leading image (i.e. the cue) was 100% predictive of the subsequent trailing image (i.e. the target). During the test phase in the scanner, the leading image was now only 50% predictive of the trailing image. The imaging results showed weaker V1 responses when the trailing image followed the predictive leading image than when it followed a non-predictive leading image (see also Alink, Schwiedrzik, *et al.*, 2010). Alink & Blank (2021) proposed that expectations regarding the target could actually be considered as a form of salience modulation, which could explain why expected targets elicited weaker occipital responses: their salience is decreased compared to the unexpected targets.

Accordingly, to date, there is no consensus regarding the mechanisms through which attention integrates target spatial statistical regularities to the spatial priority maps (e.g. see Melloni *et al.*, 2012, who found higher parietal activations for expected display configurations, vs. Won *et al.*, 2020; Zhang *et al.*, 2021, who instead reported decreased parietal activation for expected display configurations). To address this further, there are two main issues that have to be investigated. First, is the spatial representation of the target lowered, when the target is presented at an expected location (see Richter & de Lange, 2019 for related findings in feature-based attention; cf. also Alink & Blank, 2021)? And, second, if expectations regarding the target location work in a similar manner as bottom-up salience, do similar brain mechanisms govern how salience and expectation contribute to instantiating attention spatial priorities?

Here, we sought to address these issues by directly testing the interaction between physical visual salience and target-probability location. We employed a classical search task and we measured the response strength of occipital regions representing the location of target and distractors, as a function of target-probability location and target/distractor salience. At the occipital level, we expected a decreased spatial bias towards the target quadrant representation for targets presented at the HTPL versus at a LTPL if the “expectation suppression” also applied to recurring presentation of a target (rather than

distractor, see Zhang *et al.*, 2021) at a specific spatial location. On the contrary, in the context of the priority maps framework, we expected an increased spatial bias in the HTPL compared to the LTPL condition if the target representation was boosted when presented at the HTPL (Awh *et al.*, 2012; Zhang *et al.*, 2021). In addition, on the basis of previous works highlighting the role of parietal-occipital interactions in visuo-spatial attention control (Vossel, Weidner, *et al.*, 2012; Vossel, Geng, *et al.*, 2014; Beffara *et al.*, 2022), we investigated the condition-dependent changes of inter-regional connectivity (Friston, Buechel, *et al.*, 1997; McLaren *et al.*, 2012) between the dorsal parietal cortex and the occipital cortex. By manipulating independently stimulus low-level salience and statistical regularities, we tested the main hypothesis that these two factors would elicit similar changes at the brain level (see Alink & Blank, 2021), i.e. to recruit overlapping areas/networks and to trigger similar patterns of functional connectivity.

3.2 MATERIAL & METHODS

3.2.1 Participants

25 right-handed healthy adults were recruited for the study. They had normal or corrected-to-normal vision, no neurological, psychiatric or cognitive impairments and gave their written informed consent to participate in the study. The study was approved by a national ethics committee in biomedical research (Comité de Protection des Personnes: Sud-Méditerranée II, authorization ID: 2019-A00713-54). 23 participants were included in the final analyses (mean age: 25, range 19-32; 14 females). Two participants were excluded because 1 participant had excessive head movements (> 3 mm) and 1 participant moved the eyes towards the stimuli locations during the main attentional task (preventing us from obtaining stable quadrant-specific occipital responses).

3.2.2 Experimental design

The experiment was composed of a total of 5 functional imaging runs (4 runs of the main attention task, 10 min each; plus 1 localizer run, 10 min) and one anatomical scan (6 min). Visual stimuli were presented using Cogent Graphics, developed by John Romaya at the Wellcome Department of Imaging Neuroscience, running under MATLAB (The MathWorks, Natick, MA). The stimuli were projected on a screen placed at 90cm from the participant's eyes (1024 x 768 pixels; projected image size: 31.5cm height x 42cm width).

Localizer task

A localizer task was used to identify the occipital spatial representations of each of the four quadrants of the screen (TL, top-left; TR, top-right; BR, bottom-right or BL, bottom-left), where the stimuli of the main attention task were presented (see below). The

localizer visual stimuli consisted in a moving ($28^\circ/\text{s}$) array of small bars ($0.5 \times 0.1^\circ$ each). The array was only visible in a specific screen location on each stimulation block: a $3 \times 3^\circ$ square aperture centered at 7° of eccentricity from the display center located in one of the four quadrants. The aperture contained approximately 9 bars at a time. All bars were oriented either horizontally or vertically, but the target stimuli that were right/left tilted (45° from vertical). The target-bars appeared in the aperture at unpredictable times (range 1.08-3.24 sec) and the participants had to report the (right/left) tilt orientation by pressing a response-button with the index/middle finger of the right hand. Participants had to maintain eye-fixation at the center of the screen throughout the localizer scan. The stimuli were presented in each screen quadrant for blocks of 14 seconds, interleaved with 12 seconds of central fixation without any visual stimulation. Each quadrant was stimulated 6 times, in a randomized order.

Main attentional task

The main attentional task was split into 4 fMRI runs, each including 126 trials. Each trial started with a 1000ms warning phase when a central fixation dot (0.5° diameter) was displayed in a light grey color, indicating the imminent presentation of the stimulation array. This was followed by the 4-items search array that consisted in 4 oriented bars, one in each quadrant of the screen (eccentricity = 7° , size = $2.0 \times 0.5^\circ$, see Fig. 1). The array was displayed for 300ms. Each bar contained a dot either in the top or the bottom part of the bar. The target bar was tilted -25° or 25° from the vertical, while the 3 distractor bars were tilted -25° or 25° from the horizontal. The participants' goal was to indicate the up/down location of the dot placed inside the target-bar (see Fig. 1) by pressing a response-button with the index/middle finger of the right hand. The 3 distractor bars were fully irrelevant for the task at hand. Participants had up to 3000ms to give a response. The inter-trial interval was between 3000 and 4000ms (uniform distribution). Participants had to maintain eye-fixation at the center of the screen throughout the fMRI-runs.

On each trial, the 4 bars were either all of the same color (green or red, counterbalanced across participants) or included a color singleton (one green bar among three red bars, or vice-versa). This yielded the three display-conditions that served to operationalize the manipulation of stimulus-driven salience (see Fig. 1): Homogeneous Display (HD, all stimuli of the same color), Salient Target Display (STD, when the target was the color singleton) and Salient Distractor Display (SDD, when the distractor stimulus in the quadrant opposite the target was the color singleton). In order to reduce the total number of possible conditions, in the SDD condition the salient distractor always appeared in the quadrant opposite to the target quadrant. The three display-conditions were presented with equal probability.

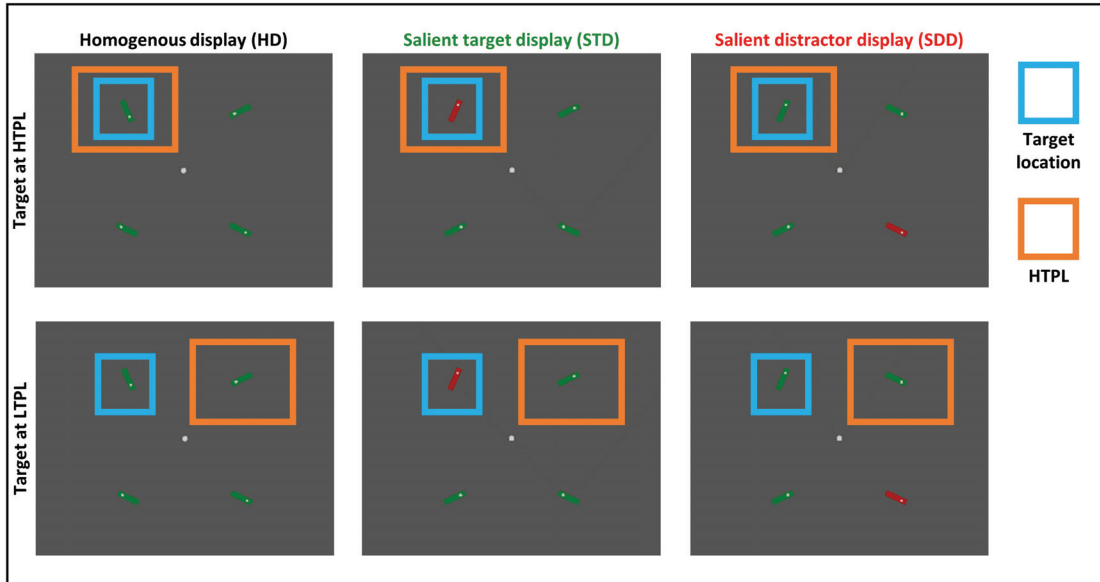


Figure 3.1: **Figure 1. The 6 main experimental conditions.**

For targets appearing in one specific quadrant (here, top-left), there were 6 possible experimental conditions (hence a total of 4 (quadrants) x 6 (conditions) = 24 conditions). The 6 main experimental conditions correspond to a 2 (statistical learning conditions) x 3 (display-configurations) design. Stimulus-driven salience is operationalized using a color singleton item: the 4 stimuli could be of the same color (HD condition), the target could be the color singleton (STD condition) or the distractor opposite to the target quadrant could be the color singleton (SDD). For each of the 3 display-configurations, the target (highlighted in blue) could occur either at a high-probability location (HTPL, 50% probability; top panels) or at a low probability location (LTPL, i.e. the 3 remaining quadrants, 16.7% probability for each position, bottom panels).

To address the effect of statistical regularities, we manipulated the probability of the target to be presented in a given screen quadrant. In each fMRI-run, the target stimulus was presented with high probability in one of the 4 quadrants (HTPL, 50%; Fig. 1, top panels) and with lower probability in the other 3 quadrants location (LTPL, 16.67% chance for each quadrant; Fig. 1, bottom panels). The HTPL quadrant was pseudorandomly assigned to a different quadrant across the 4 fMRI-runs. The combination of display-type, target-probability location, and target-location resulted in a fully-factorial design: 3 display-conditions (HD, STD, SDD) x 2 target-probability location (HTPL, LTPL) x 4 target locations (i.e. the screen quadrants: TL, TR, BR, BL).

3.2.3 Eye tracking

The gaze-position was measured throughout both the localizer scan and the 4 fMRI-runs of the main experiment. The participants' gaze was tracked using a MR-compatible EyeLink 1000 (SR Research Ltd., Mississauga, Ontario, Canada) at a sampling rate of 500Hz. Calibration was performed using the four quadrants (7° eccentricity), plus the screen center. Eye-tracking data analysis was performed using custom MATLAB scripts.

Data were extracted in a 2500ms window starting 500ms before the preparatory phase onset for each trial. These were baseline-adjusted using the median of the vertical and horizontal gaze-position during the first 500ms. We assessed the quality of each trial's data considering the percentage of data-points larger than 10° /smaller than -10° , caused by eye blinks or noisy signal. Only trials with less than 50% of these unreliable data-points (86% of the trials) underwent further analyses. In these trials, any displacement of gaze-position larger than 0.5° and lasting for at least 100ms was classified as an eye-saccade. An eye-saccade outside a central box of 2° from the center of the screen excluded the trial (10.4% of the trials with reliable data) from behavioral analyses. In addition, these excluded trials were modeled in a dedicated regressor of non-interest in the imaging analyses.

3.2.4 Behavioral analyses

At the end of the experiment, participants were asked whether they noticed anything peculiar during the experiment. They were then asked whether they noticed any pattern or regularity of the target location during the fourth fMRI-run, and to guess what was the location where most of the target were presented in this last run. Finally, they were asked to guess the sequence of HTPL across the 4 runs.

We analyzed the RTs and accuracy data for the main attentional task using linear mixed models implemented in R-studio (Bates *et al.*, 2015). For the RT analysis, trials with wrong/no/late responses and/or including losses of fixation (cf. above) were discarded from the analysis. The model included the log-transformed RTs as the dependent variable and the display-condition (with 3 levels: HD, STD & SDD), the target probability location condition (with 2 levels: HTPL, LTPL) and their interaction as the explanatory variables. For the accuracy analysis, only trials including losses of fixation were discarded. The model included the response accuracy (correct or wrong) modeled using a binomial law as the dependent variable, and the display-condition, target-probability location and their interaction as explanatory variables. Because of the repeated measures, both models also included subject-specific intercepts. All descriptive statistics reported in the results section are expressed in mean \pm standard error (SEM).

3.2.5 Image acquisition and preprocessing

T2*-weighted echoplanar images (EPI) with blood oxygen level-dependent (BOLD) contrast (interleaved multiband sequence, Multiband Factor = 2, 50 slices covering the entire brain, field of view = 220x210.4mm, Repetition Time = 1.72s, echo time = 30ms, phase encoding direction = antero-posterior, slice orientation = approx. axial, voxel size = $2.4 \times 2.4 \times 2.4\text{mm}^3$) were obtained using a 3T MRI System (Trio, Siemens). A high-resolution anatomical scan was acquired using a standard T1-weighted 3D

MP-RAGE sequence (Repetition Time = 3s, echo time = 3.8ms, voxel size = 1 x 1 x 1mm³).

The functional data were preprocessed and analyzed with the Statistical Parametric Mapping software SPM12 (Wellcome Department of Imaging Neuroscience, University College London, UK; <http://www.fil.ion.ucl.ac.uk/spm>). After discarding the first four volumes of each imaging run, images were corrected for head movements. Slice-acquisition delays were corrected using the middle slice as reference. All images were normalized to the SPM12 Tissue Probability Map and re-sampled to 2mm isotropic voxel size. Unsmoothed data were used for ROI analyses and smoothed data were used for whole-brain and psychophysiological interactions analyses.

3.2.6 Single-subject analyses

Localizer and individual Regions Of Interest (ROIs)

The procedure for the ROIs definition has been conducted as specified in Beffara and colleagues (2022). In brief, the single-subject models (GLM) included the 4 conditions corresponding to the 4 stimulated quadrants (i.e. TL, TR, BR, BL locations, blocks of 14 seconds), plus the 6 movements parameters as regressors of non-interest. These were convolved using the SPM12 “Hemodynamic Response Function”. For each participant, we tested the main effects of the side of the visual stimulation at the whole-brain level (e.g. "TL+BL > TR+BR", for left hemifield quadrants) and separated voxels responding to stimulation of the upper or the lower quadrant by using inclusive masking with the relevant effect of top/bottom stimulation (i.e. top-left quadrant: "TL > BL", and bottom-left quadrant: "BL > TL"). Contrasts were thresholded at p -uncorrected = 0.005.

These subject- and quadrant-specific responses were then split based on the Automated Anatomical Labeling atlas (AAL, Tzourio-Mazoyer *et al.*, 2002) in order to define ROIs on the basis of both quadrant-specificity and anatomically-defined occipital Brodmann areas BA17, BA18 and BA19. This resulted in a total of 12 ROIs per participant (i.e. 3 BA: BA17, BA18, BA19 x 4 quadrants: TL, TR, BR, BL). The average size of the quadrant-specific ROIs (mean number of voxels \pm SEM) was: 83.68 \pm 4.64 for BA17, 220.58 \pm 8.47 for BA18 and 215.23 \pm 10.29 for BA19.

Main task

The main attentional task data were analyzed using two separate single-subject GLMs: the first one aimed at investigating quadrant-specific responses in the occipital visual cortex (cf. subject-specific ROI analyses), while the second aimed at testing at the whole-brain level the effects of salience and target-probability location, irrespective of the target-quadrant.

In order to study the quadrant-specific responses, the first GLM comprised 24 conditions of interest given by the 2 x 3 x 4 factorial design: target-probability location (HTPL, LTPL) x display-conditions (HD, STD, SDD) x target-quadrant (TL, TR, BR, BL), plus one predictor including all trials to be excluded (no response, incorrect orientation-discrimination, reaction time out of the 200-3000ms response window and fixation-loss trials) and the 6 movement parameters. Each trial was modeled using the canonical Hemodynamic Response Function in SPM12, the event-onsets were time locked to the presentation of the stimulus display and the event-duration was 300ms. Only the parameter estimates of the 24 conditions of interest were used for the subsequent group-level analyses.

The second single-subject GLM comprised 6 conditions of interest: 2 target-probability location (HTPL, LTPL) x 3 display-conditions (HD, STD, SDD), plus one predictor including trials to be excluded from the group analyses and the 6 movement parameters. Each trial was modeled using the canonical Hemodynamic Response Function in SPM12. The event-onsets were time locked to the presentation of the stimulus display and the event-duration was 300ms. Only the parameter estimates of the 6 conditions of interest were used for the subsequent group-level analyses.

3.2.7 Group-level analyses of spatially-specific occipital responses

Target selection, salience and target-probability location

We were interested in the modulation of spatially-specific occipital responses by statistical regularities and physical visual salience. For this, we examined the activity in the ROIs representing the target-quadrant and the opposite quadrant (see Beffara *et al.*, 2022), as a function of the priority signals present in these two quadrants. To do so, we averaged the response estimates in the occipital ROIs (separately for BA17, BA18 and BA19), considering whether the represented quadrant included the target ("ROI_IN") or the distractor located opposite to the target ("ROI_OPP", where the salient distractor was presented in the SDD condition). This was done separately for the 3 display-conditions (HD, STD, SDD) and according to whether the target-quadrant was also the HTPL or not (LTPL). This resulted in a single value per subject for each ROI-type (IN/OPP), BA and experimental condition (3 display-conditions x 2 target-probability locations). A 2x2x3x3 repeated-measure ANOVA with the factors: quadrant-type (ROI_IN, ROI_OPP) x target-probability location (HTPL, LTPL) x display-condition (HD, STD, SDD) x BA-area (BA17, BA18, B19) was employed to assess the effects of statistical regularities and visual salience, and their interaction, on the quadrant-specific responses of the 3 BAs.

Spatial bias vectors

In addition to considering activity only in the occipital regions representing the quadrant (ROI_IN) and the opposite quadrant (ROI_OPP) we examined also how target, salience and target-probability location jointly affected the overall 2D representation of visual space, now considering also the activity in the ROI representing the quadrant ipsilateral to the target quadrant ("ROI_IPSI", same hemifield as the target, but different up/down location) and the contralateral quadrant ("ROI_CONTRA", opposite hemifield, but same up/down location as the target), please see Beffara *et al.*, 2022 for a detailed explanation and graphical illustrations of these analyses. Briefly, separately for each subject and BA, the activity of 4 ROIs representing the 4 quadrants was used to construct a vector that represents the direction and magnitude of the spatial bias coded by the BA. Here, separate bias vectors were constructed for the 3 display-conditions and the 2 target-probability location conditions. The data analyses considered the Euclidian distance between the subject-specific vectors and a point positioned on the diagonal corresponding to the location of the target in the frame of reference of the bias vectors (ROI_IN, 45° in the top-left quadrant, see dotted lines on Fig. 4 top panels). The point was located at the coordinates (-12; 12) which correspond to the maximum absolute value of all X and Y coordinates, across all subjects, conditions and BAs. Any increase of distance between this point and the subject-specific vector, calculated as the Euclidian distance ($\sqrt{(-12 - X)^2 + (12 - Y)^2}$), expresses a decrease of spatial bias towards the target location representation (decrease of the vector's magnitude and/or the vector points away from the target location, see Fig. 4). The effect of target-probability location and display-conditions on these distance-values were tested using repeated-measures ANOVAs and paired t-tests.

3.2.8 Whole-brain activations

Beside the modulation of the activity in occipital regions that represent the different visual quadrants (cf. section above), we also examined the effect of target-probability location and display-condition at the whole-brain level, now irrespective of the quadrant where the target was presented (see also Won *et al.*, 2020; Zhang *et al.*, 2021). The 6 contrast images resulting from the corresponding single-subject GLMs (2 target-probability locations x 3 display-conditions, see above) were entered in a group-level repeated-measures ANOVA. We then performed the relevant T-contrasts to highlight activations corresponding to the two different types of priority signals (statistical regularities: HTPL > LTPL and LTPL > HTPL; and physical salience: STD > HD, SDD > HD, SDD > STD and STD > SDD). Significant activations reported here were thresholded at p-FWE-corrected = 0.05 at the cluster level, with the cluster-sizes defined at a voxel-wise threshold of p-uncorrected = 0.005, considering the whole brain as the volume of interest. Results are visualized using SPM and MRIcro.

3.2.9 Psychophysiological interactions (PPI)

Our whole-brain analysis (cf. above) revealed joint effects of both statistical regularities and salience in the posterior parietal cortex (PPC; see Fig. 5). We sought to investigate further the possible role of the PPC in the processing of these attentional signals using analyses of effective connectivity. The gPPI toolbox ("generalized psycho-physiological interaction", McLaren *et al.*, 2012) for SPM was used to test for condition-dependent changes of inter-regional connectivity with the PPC (Friston, Buechel, *et al.*, 1997). The seed region comprised the voxels showing an effect of both target-probability location (LTPL > HTPL) and display-conditions (SDD > STD), and that were located within the anatomically AAL-defined BA7 (Tzourio-Mazoyer *et al.*, 2002). The final PPC seed region included 187 voxels. The first-level PPI model included the 6 experimental conditions (2 target-probability locations x 3 display-conditions), the subject-specific time-series of the PPC seed region, the 6 PPI regressors corresponding to the interactions between each experimental condition and the seed region, plus the 6 movement parameters.

The group analysis comprised a repeated-measures ANOVA with the 6 relevant PPI interaction-terms. We tested for the changes of the PPC coupling as a function of salience (STD > HD, SDD > HD, SDD > STD and STD > SDD) and of statistical regularities (LTPL > HTPL and HTPL > LTPL). Significant effects are reported at a threshold of p-FWE-corrected = 0.05 at the cluster level, with the cluster-size defined at a voxel-wise threshold of p-uncorrected = 0.005, considering the whole brain as the volume of interest. Our main prediction concerned the connectivity between PPC and the occipital cortex, that we expected to increase in the low target-probability condition ("LTPL > HTPL") and/or the salient distractor condition ("SDD > STD") that our whole-brain analyses associated with the activation of the PPC (see Fig.5, and Won *et al.*, 2020; Zhang *et al.*, 2021).

3.3 RESULTS

3.3.1 Behavioral data

None of the participants reported having noticed the target-probability location manipulation when asked if he/she noticed something peculiar during the experiment. When asked about the target location imbalance during the last fMRI-run, 7 participants declared that they noticed target location imbalance. When asked to guess the HTPL in the last fMRI run, 14 participants were able to correctly report the HTPL. 12 participants declared that they noticed changes of HTPL across runs. Only 2 participants out of 23 were able to report the correct sequence of HTPL across the 4 runs. Only one participant both declared that he/she noticed a change of HTPL across runs and reported the correct

HTPL sequence across runs.

The analysis of the RTs revealed a significant main effect of target-probability location, with longer RTs in LTPL than in HTPL ($F(1,9852) = 98.36$, $p < 0.001$; HTPL, 728 ± 3.09 ms; LTPL, 759 ± 3.09 ms; fixed-effect Cohen's d for the HTPL vs. LTPL comparison = 0.16) and a significant main effect of display-condition, with longer RTs in SDD than in HD and in HD than in STD ($F(2,9852) = 203.36$, $p < 0.001$; HD, 744 ± 3.77 ms; STD, 702 ± 3.43 ms; SDD, 786 ± 4.02 ms; fixed-effect Cohen's d for the STD vs. SDD comparison = 0.43). We found no significant interaction between the two factors on RTs ($F(2,9852) = 0.22$, $p = 0.80$) (Fig. 2A). Accuracy analyses showed a significant main effect of target-probability location, with poorer accuracy in LTPL than in HTPL ($\chi^2(1,10549) = 5.93$, $p = 0.01$; accuracy for: HTPL, $94 \pm 0.6\%$; LTPL, $93 \pm 0.7\%$; odds-ratio for HTPL vs. LTPL = 1.21) as well as a significant main effect of display-condition, with lower accuracy for SDD than HD and for HD than STD ($\chi^2(2,10549) = 13.22$, $p = 0.001$; accuracy for: HD, $93 \pm 0.8\%$; STD, $94 \pm 0.8\%$; SDD, $92 \pm 0.8\%$; fixed-effect odds-ratio for STD vs. SDD = 1.42). Here also, no significant interaction was found between target-probability location and display-condition ($\chi^2(2,10549) = 0.02$, $p = 0.99$) (Fig. 2B). The results demonstrate that target salience facilitates discrimination, while distractor salience reduces search performance; and that target-probability location also affects performance, facilitating target-discrimination at expected locations and reducing performance at unexpected locations (Melloni *et al.*, 2012; Ferrante *et al.*, 2018; Won *et al.*, 2020).

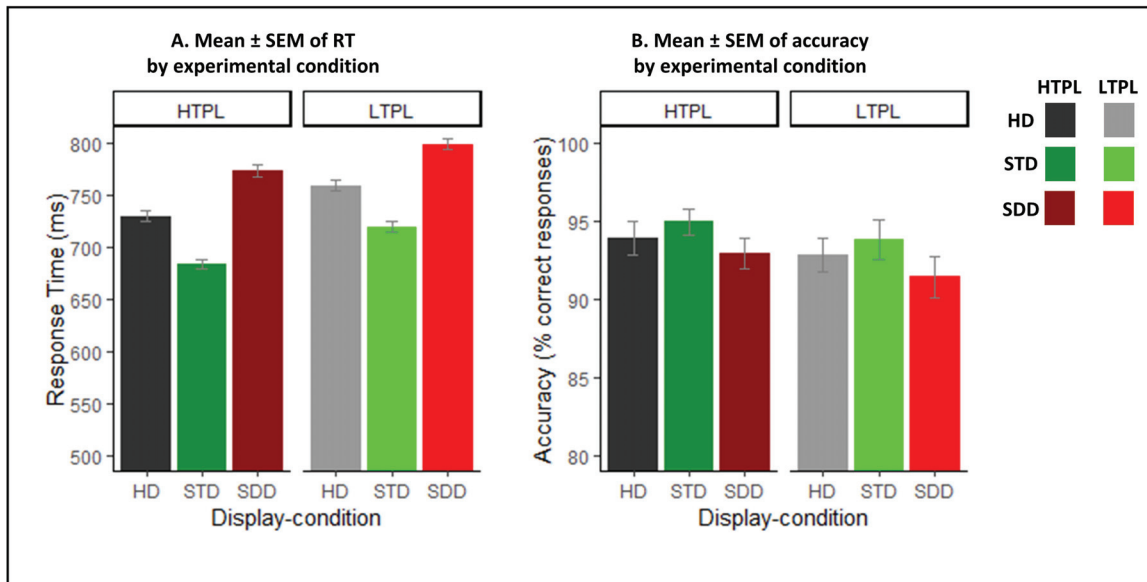


Figure 3.2: **Figure 2. Behavioral results for the 6 main experimental conditions.** **A** - The RTs (mean \pm SEM) showed significant effects of both display-condition/visual salience (STD < HD < SDD) and of target-probability location (HTPL < LTPL), without any interaction between the two factors. **B** - The accuracy data (mean \pm SEM) revealed an analogous pattern of results, with significant effects of display-condition and target-probability location, but no interaction.

3.3.2 Attentional priority signals modulate activity in the occipital cortex

Regions representing the target location (ROI_IN) and the opposite quadrant (ROI_OPP)

Our first aim was to assess how multiple attentional signals present in the visual field affect quadrant-specific spatial representations in the occipital cortex. First, we considered activity of the occipital region representing the current target location (ROI_IN) and the region representing the opposite quadrant, where the salient distractors were presented in the SDD condition (ROI_OPP). The corresponding 2x3x2x3 ANOVA (ROI_IN/ROI_OPP x display-condition x target-probability location x BA) revealed a significant main effect of display-condition ($F(2, 818) = 6.21, p = 0.002, \eta^2p = 0.02$), a significant main effect of ROI-type (ROI_IN vs. ROI_OPP) ($F(1,818) = 104.33, p < 0.001, \eta^2p = 0.12$) that corresponds to the effect of target selection, and a significant main effect of BA ($F(2,818) = 453.97, p < 0.001, \eta^2p = 0.54$); see Fig. 3 and Table 1. The ROI-type x display-condition and the ROI-type x BA interactions were also significant ($F(2,818) = 5.22, p = 0.006, \eta^2p = 0.01$ and $F(2,818) = 6.18, p = 0.002, \eta^2p = 0.02$, respectively). All other effects were non-significant ($p > 0.09$).

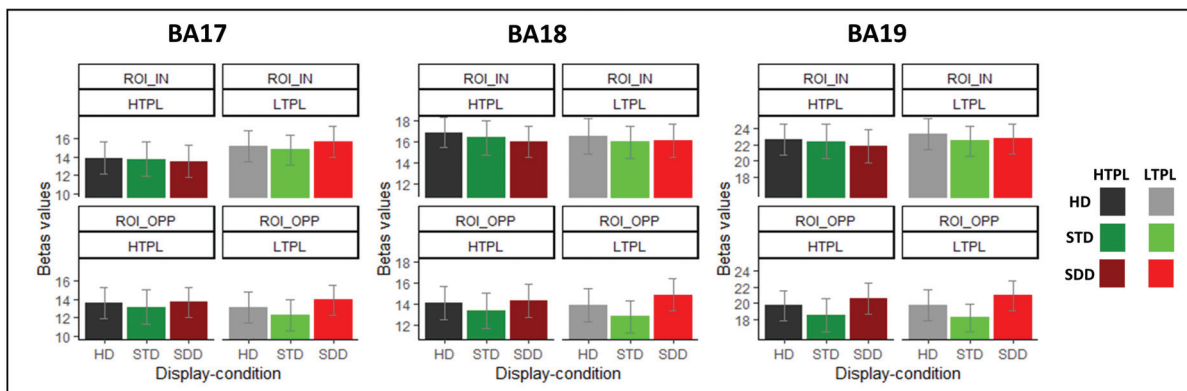


Figure 3.3: **Figure 3. Local responses in ROI_IN and ROI_OPP (mean \pm SEM) as a function of display-conditions and target-probability locations.**

Left panel shows responses in BA17, middle panel shows responses in BA18 and right panel shows responses in BA19. Grey colors are used for responses in HD, green colors for STD and red colors for SDD. Darker colors are for HTPL, brighter colors are for LTPL.

In order to disentangle the two aforementioned interactions we performed pairwise contrasts with only the factors of interest. First, we performed t-contrasts between all combinations of display-conditions, separately for ROI_IN and ROI_OPP. We found no significant effect of display-condition in ROI_IN (all $p > 0.82$). By contrast, for ROI_OPP we found a significant effect of SDD minus STD (compare green and red bars on Fig. 3, bottom-panels “ROI_OPP”), $t = 4.56, p < 0.001, \text{Cohen's } d = 0.58$; all other $p > 0.08$).

These results indicate that visual salience modulated primarily the activity associated with the representation of the distractor location, rather than the representation of the target location. Second, we performed t-contrasts between ROI_IN and ROI_OPP, separately for the 3 tested BA. These comparisons were significant for all BA: ROI_INBA17 versus ROI_OPPBA17, $t = 3.20$, $p = 0.018$, Cohen’s $d = 0.46$; ROI_INBA18 versus ROI_OPPBA18, $t = 6.38$, $p < 0.001$, Cohen’s $d = 1.14$; ROI_INBA19 versus ROI_OPPBA19, $t = 8.11$, $p < 0.001$, Cohen’s $d = 1.39$ (compare bars on Fig. 3 top-panel “ROI_IN” with bars on bottom-panel “ROI_OPP”). This shows that the target selection (responses in ROI_IN > responses in ROI_OPP) was present in all 3 BA, albeit with an increasing magnitude from BA17 to BA19, cf. significant interaction between ROI-type and BA.

	HTPL		LTPL	
BA17	ROI_IN	ROI_OPP	ROI_IN	ROI_OPP
HD	13.91 ± 1.71	13.62 ± 1.65	15.13 ± 1.69	13.08 ± 1.68
STD	13.77 ± 1.88	13.16 ± 1.87	14.77 ± 1.60	12.30 ± 1.66
SDD	13.51 ± 1.76	13.69 ± 1.63	15.66 ± 1.65	13.94 ± 1.60
BA18				
HD	16.81 ± 1.42	14.16 ± 1.55	16.49 ± 1.72	13.96 ± 1.57
STD	16.34 ± 1.62	13.42 ± 1.69	15.90 ± 1.57	12.86 ± 1.51
SDD	15.96 ± 1.48	14.33 ± 1.57	16.06 ± 1.60	14.94 ± 1.55
BA19				
HD	22.67 ± 1.88	19.74 ± 1.79	23.30 ± 1.91	19.75 ± 1.90
STD	22.40 ± 2.12	18.53 ± 2.00	22.44 ± 1.77	18.23 ± 1.73
SDD	21.88 ± 2.03	20.63 ± 1.89	22.73 ± 1.82	20.98 ± 1.82

Figure 3.4: **Table 1. Mean ± SEM of the mean parameters estimates of the GLM (beta values) as a function of BA, ROI-type, target-probability location and display-condition.**

In sum, we found a significant effect of target selection, with larger activation of the target quadrant representation (ROI_IN) than the distractor representation (ROI_OPP). This effect was progressively larger from BA17 to BA19. The second main result was the modulation the distractor representation (ROI_OPP), as a function of the display-condition: activity was higher when the distractor represented by ROI_OPP was salient than when the target was salient. The analyses of activity in ROI_IN and ROI_OPP did not reveal any significant effect of target-probability location (HTPL/LTPL).

Modulation of 2D occipital spatial representations: spatial bias vector analysis

Results concerning the local activity in areas representing the target and the opposite distractor (ROI_IN and ROI_OPP) did not reveal any significant effect of target-probability location, but it should be noticed that these analyses did not consider the representations of the whole visual display. To do this, we considered a complementary analysis approach that takes into account the activity of all 4 ROIs that represent the 4 quadrants containing the search items (cf. methods section, and Beffara *et al.*, 2022).

Using a 3x2x3 ANOVA we examined the effects display-condition, target-probability location and BA on the spatial bias vectors.

The results revealed a significant main effect of display-condition ($F(2,406) = 23.38$, $p < 0.001$; $\eta^2p = 0.11$), a main effect of target-probability location ($F(1,406) = 24.26$, $p < 0.001$; $\eta^2p = 0.06$), a main effect of BA ($F(2,406) = 33.78$, $p < 0.001$; $\eta^2p = 0.15$), as well as a significant target-probability location x BA interaction ($F(1,406) = 4.52$, $p < 0.001$; $\eta^2p = 0.05$). All other main effects or interactions were not significant (all $p > 0.07$), see Table. 2 and Fig. 4. We investigated the significant effects further using pairwise t-contracts.

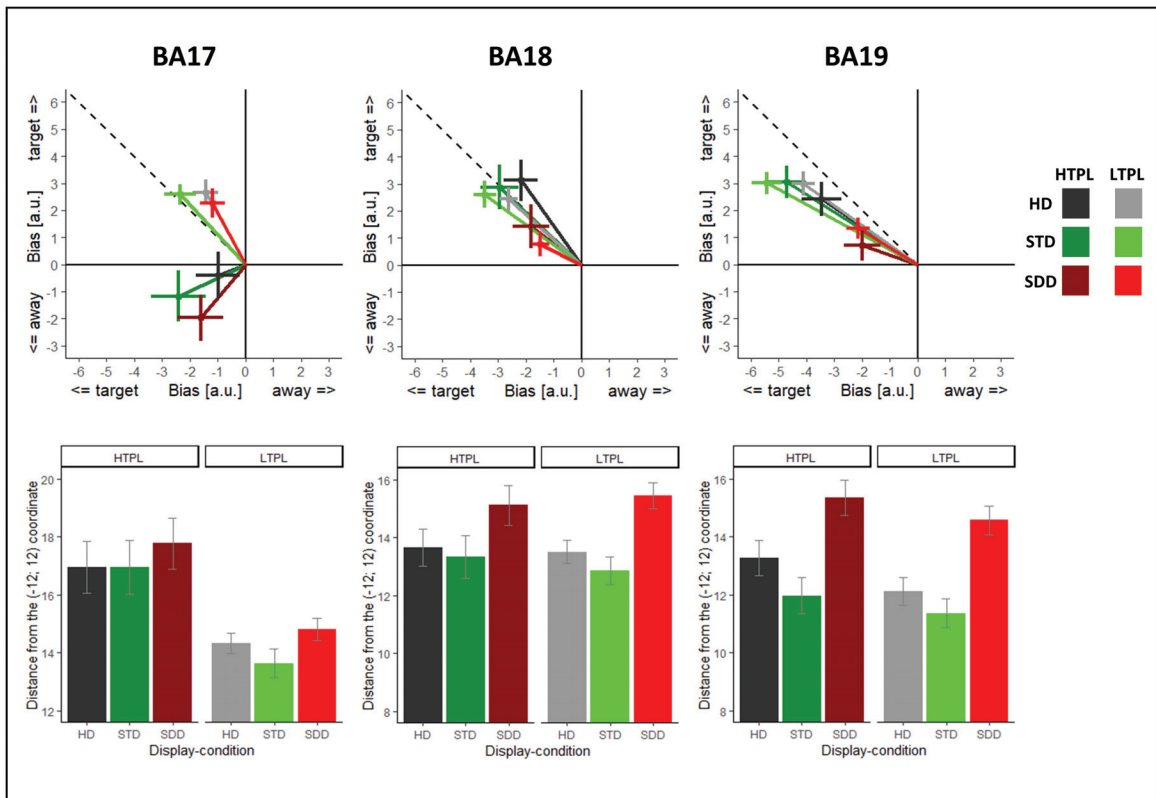


Figure 3.5: **Figure 4. Spatial bias vectors as a function of display-condition and target-probability location.**

Top panels show spatial bias vectors in BA17, BA18 and BA19 (left to right). The 45° dotted line represents the direction of the target-quadrant, in the arbitrary frame of reference of the bias vectors. The vectors represent the overall spatial bias in the occipital cortex, computed using the combined activity of the 4 ROI that represent the visual location of the search items (target location, opposite, ipsilaterally and contralateral: ROI_IN, ROI_OPP, ROI_IPSI, ROI_CONTRA). Bottom panels show mean distance (\pm SEM) between the point in the target quadrant (-12; 12) and spatial bias vectors for the 2 target-probability locations and the 3 display-conditions. Black color is used for the HD condition, green for STD and red for SDD. Darker color are vectors in HTPL condition and brighter color are vectors in LTPL condition.

The pairwise comparisons between HTPL vs. LTPL, separately for the 3 BAs, revealed

a significant effect of target-probability location in BA17 only. The spatial bias vector was more distant from the target location in HTPL than in LTPL, which explains the target-probability location \times BA interaction. In Fig. 4, this can be seen on the top-left panel where dark-colored vectors (HTPL) are further away from the black dotted-line than bright-colored vectors (LTPL). This means that presenting the target at HTPL results in a loss of spatial bias towards the target quadrant in BA17 (see Table 2 for statistics, and see dark-colored bars vs. bright-colored bars on Fig. 4 bottom-left panel). This suggests that target-probability location affects early stages of the visual processing. Pairwise comparisons between the 3 display-conditions revealed that salient distractors decreased the bias towards the target location compared to both homogeneous displays (higher distance values for SDD vs. HD) and salient target displays (SDD vs. STD), while salient targets did not significantly strengthen the bias towards the target location representation (STD vs. HD), see Table 3. In BA18 and BA19, the reduction of the spatial bias for the SDD condition consisted primarily in a reduction of the bias magnitude, compared with the STD and HD conditions (compare the red-SDD vectors with the green-STD and gray-HD vectors in Fig. 4A, see also Fig. 4B). These results show that salience is represented across all tested BA, but only decreasing the spatial bias towards the target representation when associated the distractor.

Finally, pairwise comparisons between the 3 BAs, irrespective of condition, showed that the spatial biases towards the target-quadrant increased progressively from early to higher-level visual areas (BA17 < BA18 < BA19, see Table 2).

Comparison	t-value	p-value	Cohen's d
HTPL _{BA17} versus LTPL _{BA17}	6.45	< 0.001	0.62
HTPL _{BA18} versus LTPL _{BA18}	0.23	0.99	
HTPL _{BA19} versus LTPL _{BA19}	1.86	0.43	
HD versus STD	1.91	0.13	
HD versus SDD	-4.73	< 0.001	-0.72
STD versus SDD	-6.64	< 0.001	-0.75
BA17 versus BA18	5.38	< 0.001	0.47
BA18 versus BA19	2.70	0.02	0.31
BA17 versus BA19	8.07	< 0.001	0.69

Figure 3.6: **Table 2. Statistics of the pairwise comparisons of the vectors' "distance" values between target-probability location conditions, between display-conditions and between BA.**

In sum, we found evidence that target-probability location modulates the spatial bias in areas BA17, with a loss of spatial specificity towards the target position in the HTPL condition. In addition, we found that salient distractors reduced the attention bias towards the target location (SDD vs. HD; see also Sprague *et al.*, 2018; Beffara *et al.*, 2022). These results provide evidence regarding the modulation of the spatially-specific occipital responses by statistical regularities, and indicate that the spatial bias analysis can capture effects that were not accounted for in the ROI_IN/OPP analysis (cf. previous

section).

3.3.3 Whole-brain analyses

Besides occipital spatial bias modulations, previous studies pointed the parietal cortex as a key region involved in the processing of salience and statistical regularities (e.g. see Won *et al.*, 2020; Zhang *et al.*, 2021 and see Geng, 2014; Geng & Duarte, 2021 for reviews). Accordingly, we performed a whole-brain group analysis using a 2x3 (target probability location x display-conditions) ANOVA. The direct comparison of LTPL > HTPL yielded a significant activation in the bilateral PPC (left and right Superior Parietal Lobule, see Table 3), left dorsal frontal cortex (left Middle Frontal Gyrus, see Table 3), right Supramarginal Parietal Gyrus as well as the anterior part of the left occipital cortex, mostly located in BA19. When comparing SDD > STD, we found significant clusters of activation in areas of the fronto-parietal network (Bilateral Middle Frontal Gyrus and bilateral Superior Parietal Lobule) and in the anterior part of the left occipital cortex (see Table 3), mostly located in BA19.

Comparison	Region	Cluster size (voxels)	Cluster-level p-value (FWE-corrected)	Z-score	MNI-coordinates			
					x	y	z	
SDD > STD	L Middle Frontal Gyrus	847	< 0.001	5.38	-28	-2	52	
	L Middle Frontal Gyrus	667	0.001	5.04	-28	-2	52	
	R Inferior Frontal Gyrus			3.78	14	28	30	
	L Lateral Occipital Gyri	2300	< 0.001	4.41	-38	-78	10	
	R Inferior Frontal Gyrus			4.16	-28	-68	28	
	L Superior Parietal Lobule			4.14	-26	-54	56	
	R Superior Parietal Lobule	416	0.017	4.11	24	-52	54	
	R Middle Frontal Gyrus	416	0.017	3.94	20	0	52	
	LTPL > HTPL	L Lateral Occipital Gyri	1401	< 0.001	4.57	-48	-64	8
		R Superior Parietal Lobule	1007	< 0.001	4.54	18	-56	64
R Supramarginal Parietal Gyrus				3.63	36	-30	36	
L Superior Parietal Lobule		2852	< 0.001	3.84	-36	-40	56	
L Middle Frontal Gyrus				3.72	-26	-8	58	

Figure 3.7: **Table 3. Statistics of the whole-brain activations.**

Thus, at the whole-brain level, we found that the processing of physical salience and statistical regularities rely on the activation of the same portion of the PPC (see overlaps in the parietal cortex, rendered in purple-color in Fig. 5). The signal plot in Fig. 5 shows that, in the PPC, activity increased in the presence of a distractor singleton compared to displays including a salient target (SDD vs. STD, red vs. green bars). In this region, targets appearing at unexpected locations elicited greater responses than targets appearing at the expected location (LTPL vs. HTPL, bars 4-6 vs. bars 1-3). These results suggest that increasing the competition between spatial locations, by including distractor singletons and by presenting targets at unexpected locations (LTPL), increases the requirement of engaging the dorsal attention control network.

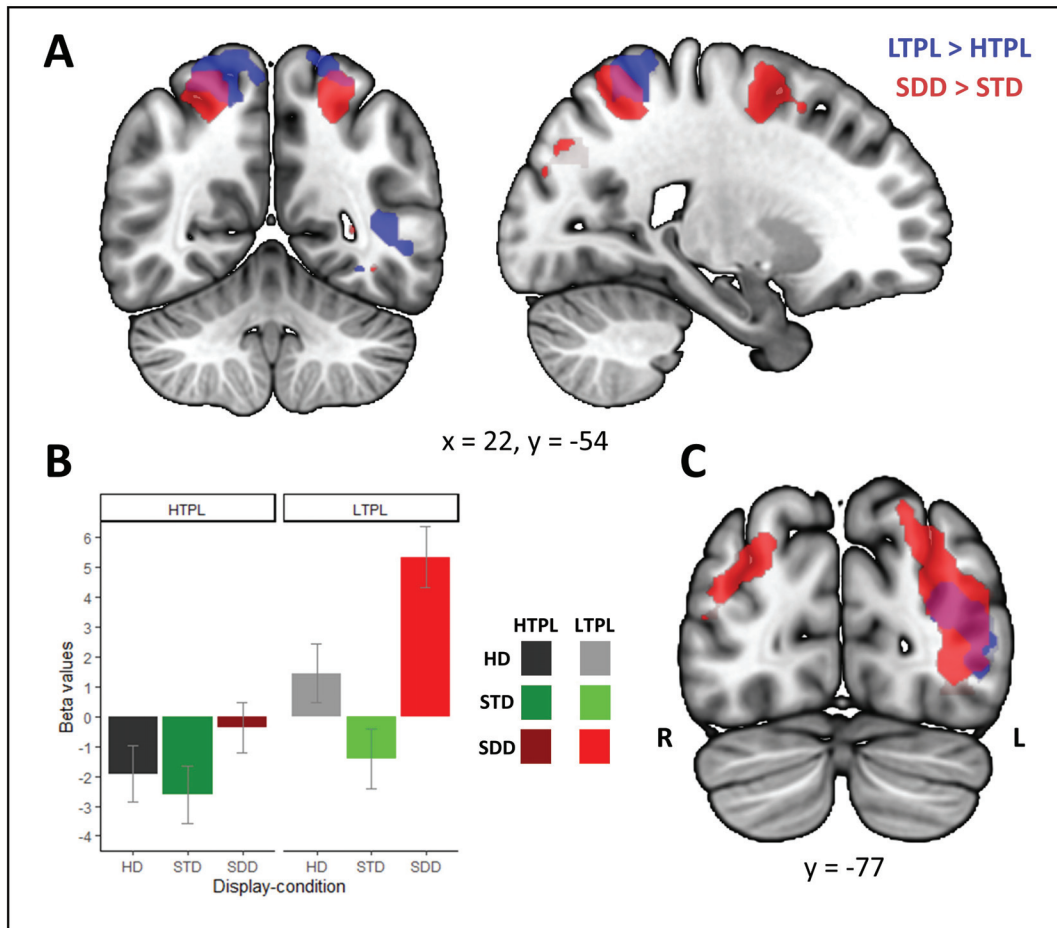


Figure 3.8: **Figure 5. Whole-brain activations associated with salient distractors (SDD vs. STD) and targets at unexpected locations (LTPL vs. HTPL).**

A – Coronal and sagittal sections showing the overlap between salience (SDD > STD) and target-probability location (LTPL > HTPL) in the posterior parietal cortex. **B** – Mean (\pm SEM) parameters estimates (Beta values) for the voxels in the posterior parietal cortex showing both an effect of salience and of target-probability location (cf. region rendered in purple-color, in panel A). **C** - Occipital overlap between salience (SDD > STD) and target-probability location (LTPL > HTPL). Activation clusters are rendered a p-FWE-corrected = 0.05 at the cluster level, with cluster sizes estimated at p-uncorrected = 0.005.

3.3.4 Psychophysiological interactions

Finally, we explored possible links between the effects of the display-condition and the target-probability location in the PPC (cf. whole-brain analysis, and Fig. 5A), with the modulatory influences that we observed in the occipital visual cortex (see Fig. 3-4). For this, we carried out a psycho-physiological interaction analysis using the voxels in PPC that showed an overlap for the SDD > STD and the LTPL > HTPL contrasts (see Fig. 5A purple-color, and Methods Section). The contrast testing for increased interregional coupling in SDD vs. STD did not reveal any significant effect. By contrast, the comparison between LTPL and HTPL showed a significant cluster in the left middle occipital gyrus, extending ventrally to the inferior occipital gyrus (MNI x, y, z = -32,

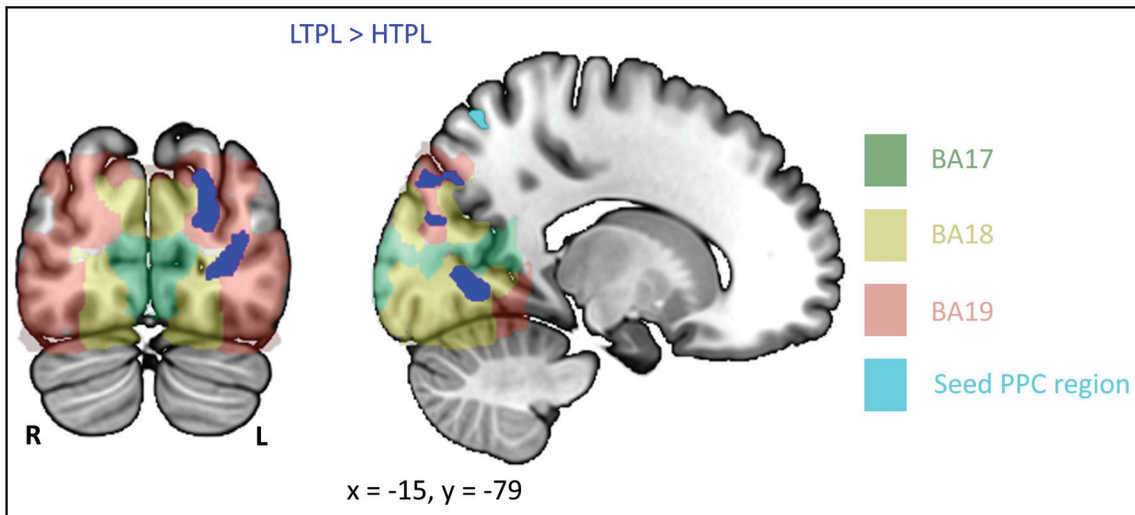


Figure 3.9: **Figure 6. Results of the functional connectivity analyses with seed region in the PPC.**

The PPI analysis revealed increased connectivity between the PPC seed region (rendered in cyan) and areas in the left occipital cortex for target presented at the low vs. high probability-location (LTPL > HTPL, rendered in blue). At a lower, uncorrected threshold similar effect were observed also in symmetrical regions of the right occipital cortex (not shown). The significant cluster in the occipital cortex included voxels in BA18 and BA19, but not in BA17. The PPI effect is rendered at a p-FWE-corrected = 0.05 at the cluster level, with cluster sizes estimated at p-uncorrected = 0.005.

-84, 16; Z-value = 5.1, p-FWE-corrected = 0.004, n. voxels = 471). A second cluster was found in the left superior occipital gyrus, albeit this did not reach statistical significance at the whole-brain level (MNI x, y, z = -20, -82, 24; Z-value = 4.1, p-FWE-corrected = 0.087, n. voxels = 253). At uncorrected threshold (p-uncorrected = 0.005) symmetrical clusters were found in the right hemisphere. Additional analyses specifically tested for change of PPC coupling (LTPL > HTPL) in the 3 tested BAs. Using the anatomical ROI, the small-volume correction procedure revealed significant effects in BA18 (peak at MNI -32 -84 14, p-FWE-corrected at the voxel level = 0.014, Z-value = 4.46) and BA19 (peak at MNI -32 -84 16, p-FWE-corrected at the voxel level = 0.001, Z-value = 5.10), but not in BA17.

These additional analyses show that the target-probability location modulates the connectivity between the PPC and high-order occipital visual areas, while there was no evidence of changes of connectivity between the PPC and the primary visual cortex (BA17). This suggests that reduction of spatial bias associated with the HTPL condition that we found in BA17 (cf. "spatial bias vector" results, above) may arise via local mechanisms, without any contribution of the dorsal attention control network (here the PPC, see Discussion section).

3.4 DISCUSSION

In the current study we investigated how the presence of multiple attention biasing signals (goals, physical salience, statistical regularities) jointly shape visual representations in the occipital cortex. We used a search task including 4 items displayed each in one of the four screen quadrants and tested how the spatial distribution the different attentional signals modulated activity through the visual hierarchy (Melloni *et al.*, 2012; Adam & Serences, 2021). Moreover, we conducted whole-brain analyses and analyses of functional connectivity with the aim of linking changes at the occipital level with activity in higher-order attention control regions in the fronto-parietal cortex (see Won *et al.*, 2020). Our results showed that goals, physical salience and statistical regularities modulate spatial representations throughout the visual hierarchy, with statistical regularities affecting early stages of stimulus processing (activity in area BA17) and salience affecting all stages. The whole-brain analyses revealed overlapping effects of statistical learning (LTPL > HTPL) and salience (SDD > STD) in the posterior parietal cortex (PPC), that subsequent analyses of inter-regional connectivity further linked with the changes observed in the occipital cortex. Overall, this pattern of results indicates that statistical regularities and salience engage overlapping brain regions, but also that the underlying processing mechanisms result in different signatures at the occipital level.

3.4.1 Effects of statistical regularities and visual salience on behavioral performance

In line with our predictions, the analyses of the behavioral data showed that both statistical regularities and visual salience affected performance, with targets presented at expected locations (HTPL) associated with higher accuracy and faster RTs than targets presented at unexpected locations (LTPL); and salient targets and salient distractor leading to better and poorer behavioral performance respectively. These results are consistent with a previous study (ferrante2017) that also showed a reduction of search performance both by salient distractors and upon the presentation of targets at LTPL. Nonetheless, these results appear at odds with other studies that instead reported no effect of salient distractors, indicating that these can be fully suppressed (e.g. see Melloni *et al.*, 2012; Geng, 2014; Sprague *et al.*, 2018; Won *et al.*, 2020; Geng & Duarte, 2021; Beffara *et al.*, 2022). This inconsistency may be related to differences in how voluntary/strategic attention was deployed during search. In Beffara and colleagues (2022), the task included 100%-predictive spatial cues that were presented before the display array, so that the participants knew in advance where exactly the target would appear. Thus, the participants could strategically suppress distractors processing at the uncued locations. In Melloni and colleagues (2012), there were no explicit spatial cues, but in a subset of experimental runs the participants knew whether or not the search display would contain a salient item (blocked presentation of the HD, STD or SDD condition, throughout the whole run).

Indeed, the results showed better search performance in blocked-runs compared with the mixed-runs, indicative of a more efficient distractor suppression when participants could predict that the search array would include a salient distractor (Melloni *et al.*, 2012).

Unlike here, Ferrante and colleagues (2018) reported also a significant interaction between target-probability location and display-condition: the increase of the RTs due to the presence of a salient distractor was more important when the target was at LTPL compared with HTPL. A possible explanation for this is that Ferrante and colleagues' (2018) study included only 2 display-conditions (HD and SDD), while here there were 3 different display-conditions (HD, STD, SDD). With only 2 display-conditions the participants may learn that when the display contains a salient item, this will always be a task-irrelevant distractor. We suggest that this learning process interacts with the manipulation of target location probability (HTPL/LTPL), yielding to the observed interaction at the behavioral level. By contrast, with the inclusion of the salient target display (3 display-conditions, here), the presence of a salient stimulus does not provide any information about the relevance/irrelevance of the salient stimulus (target or distractor). In this situation, there could be no additional salience-related learning process and no further interaction with the main manipulation of target location probability.

In sum, our behavioral findings demonstrate that both statistical regularities and stimulus-driven salience affect the allocation of spatial processing priorities. This indicates that in the absence of any strong endogenous drive (cf. Sprague *et al.*, 2018; Beffara *et al.*, 2022, who used 100%-predictive cues), stimulus-driven salience is not fully suppressed and does contribute to the guidance of spatial attention.

3.4.2 Occipital spatial representations are modulated according to target selection, statistical regularities and stimulus-driven salience

The biased competition model of (visual) attention control (Desimone & Duncan, 1995; Duncan *et al.*, 1998) posits that multiple visual stimuli enter competition for attentional processing resources, based on their spatial location and their behavioral relevance (low-level salience, task relevance, etc). Here we show that the activity in occipital regions that represent the stimulus location/quadrant is modulated according to the different types of attention signals (task-relevance, salience and statistical regularities). This implies a role the occipital cortex in attention control and the coding of processing resources. Previous neuroimaging studies have shown that activity in the occipital cortex increased when a target - compared to a distractor - is presented at the represented location (Melloni *et al.*, 2012; Sprague *et al.*, 2018; Beffara *et al.*, 2022). Here, we replicated this effect of task-relevance showing that the target representation (ROI_IN) had a higher activity than the

distractor representation (ROI_ OPP) in all BAs (main effect of ROI-type, see also Fig. 3). This highlights that the target selection bias occurs along the entire visual hierarchy (see also Melloni *et al.*, 2012; Sprague *et al.*, 2018; Beffara *et al.*, 2022, for similar results).

Our main aim here was to investigate how statistical spatial regularities and physical visual salience signals affect spatially-specific activity in the visual cortex, along with the target selection bias. On the basis of our previous work (Beffara *et al.*, 2022), we tested how the target selection bias changed according to spatial regularities of target location and the display-conditions, the latter allowing us to assess the effect of salience. First, we examined quadrant-specific occipital responses in the regions representing the target location (ROI_IN) and the opposite quadrant (ROI_ OPP, where the salient distractor was presented in the SDD condition), separately for BA17, BA18 and BA19. This revealed a significant ROI-type (ROI_IN/ROI_ OPP) x display-condition (HD/STD/SDD) interaction. While ROI_IN responses were not significantly affected by the display-conditions, salience was found to affect responses in ROI_ OPP. Specifically, in the ROI_ OPP we found lower responses in the STD condition (i.e. when the salient stimulus was in the ROI_IN) than in SDD condition (salient stimulus now represented in ROI_ OPP). This demonstrates that the occipital cortex is involved in salience processing and that it does so in a spatially-specific manner (see also Melloni *et al.*, 2012; Sprague *et al.*, 2018; Beffara *et al.*, 2022).

This effect of physical visual salience is commonly referred to as “stimulus-driven” or “bottom-up” salience, because it arises from the low-level features of the stimuli (color-singleton here) (e.g. Corbetta & Shulman, 2002; Beck & Kastner, 2005). Models of visual salience propose that the low-level visual features (orientation, contrast, colors, etc) are first extracted in parallel, independently from each other, and then combined into saliency maps (e.g. see Itti & Koch, 2001). This is supported by the fact that occipital regions mostly respond to specific features (e.g. stimulus orientation in BA17, Hubel & Wiesel, 1959; contrast-coding in V1-V3, Betz *et al.*, 2013), and thus cannot compute saliency maps encompassing multiple low-levels features. This implies that responses to salience (see “saliency maps”, Itti & Koch, 2001) should be observed in areas where all low-levels features are summed into a single map (“feature-agnostic saliency map” in Veale *et al.*, 2017). Indeed, while there is some evidence that salience can affect activity in primary visual areas (e.g. V1/BA17 in Chen *et al.*, 2016), imaging and electrophysiology studies (Yoshida *et al.*, 2012, and see Veale *et al.*, 2017 for a review) showed that BA17/V1 might contribute only to the computation of orientation (Yoshida *et al.*, 2012) and luminance-contrasts (Betz *et al.*, 2013). Higher-level visual areas are more plausible candidates of saliency maps (e.g. V4, part of BA19, Veale *et al.*, 2017). Accordingly, the salience effects observed at multiple levels of the visual processing (Melloni *et al.*, 2012; Beffara *et al.*, 2022, and the current results) are likely to emerge

from computations taking place in higher visual areas (i.e. BA19 here) that then affect earlier visual areas via feedback signaling (Veale *et al.*, 2017).

In the current study, we found a significant effect of display-condition that boosted ROI_OPP activity when a salient distractor was presented in the corresponding screen quadrant, consistent with previous studies (Melloni *et al.*, 2012; Won *et al.*, 2020; Beffara *et al.*, 2022, cf. Fig. 3), but no significant changes in ROI_IN. Consistent with this, we found that the spatial bias was reduced in SDD compared to HD, but that the bias was not significantly increased in STD compared to HD. This suggests that salience primarily affects spatial occipital responses when stimuli are not attended (i.e. responses in ROI_OPP here), possibly because target-related activity (ROI_IN) was already boosted due to the presence of the target in the corresponding screen quadrant. Thus, the differential activity between regions representing the target and the distractor, may best account for the computation of attentional priorities in the occipital cortex (see Melloni *et al.*, 2012; Beffara *et al.*, 2022).

By contrast with the effect observed for physical visual salience, the target-probability location did not significantly modulate activity neither in ROI_IN nor in ROI_OPP. This was at odds with our initial predictions that targets at HTPL would either result in a reduction of activity for the ROI_IN (“expectation suppression” phenomenon; Richter & de Lange, 2019; Alink & Blank, 2021) or in an enhancement (discussion in Zhang *et al.*, 2021, and see Awh *et al.*, 2012; Ferrante *et al.*, 2018; Theeuwes, 2018). Nonetheless, the analysis of the ROI_IN/ROI_OPP activity does not capture global biases of the representation of space in the occipital cortex. To reveal such distributed changes, we computed spatial bias vectors (see Beffara *et al.*, 2022) that enabled us to reveal the effect of statistical regularities, primarily in area BA17. Specifically, these analyses showed a loss of directional specificity of the attentional bias in HTPL compared to LTPL (Fig. 4). This finding is consistent with the “expectation suppression” account, positing that responses to expected stimuli are lower than responses to unexpected stimuli (Richter & de Lange, 2019; Alink & Blank, 2021; Zhang *et al.*, 2021). This account had never been directly tested in the context of spatial attention tasks because previous studies (Won *et al.*, 2020; Adam & Serences, 2021; Zhang *et al.*, 2021) focused on activity related to salient distractor stimuli. These previous studies could not disentangle two distinct mechanisms. On the one hand, any expectation-related reduction of activity in regions that represent the distractor may indicate that expected distractors are suppressed proactively via top-down processes, so as to reduce their ability to capture attention (Won *et al.*, 2020; Adam & Serences, 2021; Geng & Duarte, 2021; Zhang *et al.*, 2021). But, on the other hand, the very same effect can be interpreted as evidence of sensory expectation suppression mechanisms taking place locally in the occipital cortex, related to the repeated presentation of a same stimulus (i.e. repeated presentation of

the salient distractor in Won *et al.*, 2020; Adam & Serences, 2021) at a specific location (the high-probability location of the salient distractor in Zhang *et al.*, 2021; see Alink & Blank, 2021 for a review). Our findings are consistent with the view according to which the expectation suppression observed for the high-probability location of the salient distractor in Zhang and colleagues (2021) also applies to targets (see also Richter & de Lange, 2019 for consistent results in non-spatial attentional tasks). The latter suggests that the suppression mechanism observed in Zhang and colleagues (2021), Won and colleagues (2020) and Adam and colleagues (2021) was presumably not solely an effect of proactive distractor suppression, but also a sensory expectation suppression effect: here we also found a reduction of the spatial bias for expected targets in BA17, which was actually associated with better behavioral performances, showing that attentional priority towards the target was higher in HTPL compared to LTPL.

The processing of visual salience (display-condition factor) induced changes across all BAs (see Discussion above) while the processing of target probability locations induced spatially-specific changes in BA17 only (cf. Fig. 4). A possible explanation of this result is that the low-level feature upon which the target was detected was the stimulus orientation, which is coded in V1/BA17 (see Hubel & Wiesel, 1959; Yoshida *et al.*, 2012) and triggered expectation suppression at that stage of processing. Nonetheless, we also found significant changes in activity in occipital areas outside BA17 (cf. Fig. 5, and whole-brain results). This may be related to the fact that in BA18 and BA19, the size of the receptive field is higher than in BA17 (Dumoulin & Wandell, 2008; Kay *et al.*, 2013), which reduced the probability to observe spatially-specific sensory expectation suppression in these BAs.

3.4.3 Statistical regularities and physical visual salience beyond the occipital visual cortex: the contribution of the posterior parietal cortex

Although our main hypotheses concerned the modulation of quadrant-specific activity in the visual cortex, we also sought to explore the possible role of other regions using whole-brain analyses and inter-regional connectivity. The main result of the whole-brain analyses was that both $SDD > STD$ and $LTPL > HTPL$ contrasts revealed significant activation in the posterior parietal cortex, part of the dorsal frontoparietal attention control network (cf. Fig. 5). In a previous study, Zhang and colleagues (2021) found an increase of activity in the SPL when a distractor was presented at an unexpected location compared to an expected location. Similarly, Won and colleagues (2020) found an increased IPS activity when a salient distractor was present in the display compared to when there was no salient distractor. Our current results confirm and extend Won and colleagues' (2020) and Zhang and colleagues' (2021) findings showing maximal activation of the PPC, either when the display contained a salient distractor (as opposed

to a salient target; $SDD > STD$) or when the target was presented at a low probability location ($LTPL > HTPL$: see also rightmost bar, in Fig. 5B). This suggests that the dorsal frontoparietal network is more likely to be recruited when salient distractors strongly compete/interfere with the target processing or when the target is presented at unexpected locations.

We sought to link the co-occurring effects of statistical regularities and salience in the PPC (cf. overlap in Fig. 5A) with our main findings in the occipital cortex, using analyses of inter-regional connectivity. The results of the whole-brain analysis of connectivity showed that functional coupling between PPC and BA18, and PPC and BA19, was significantly increased in the LTPL condition ($LTPL > HTPL$), while this was not the case in BA17. This provides us with further evidence that expectation suppression taking place early in the visual path (V1/BA17) does not rely on interactions with the dorsal attentional network, but is rather controlled locally (see above, and Alink & Blank, 2021). However, the significant effects between the PPC and BA18/BA19 nuances the top-down/bottom-up dichotomy, indicating that, at least for the “statistical regularity” signals, the processing of attentional priorities depends on a mixture of both local computations in BA17 and occipito-parietal interplay (PPC-BA18 and PPC-BA19) mechanisms.

The analyses of inter-regional connectivity also tested whether the PPC coupling changed as a function of salience. Specifically, we tested any connectivity increase when the display contained salient distractors ($SDD > STD$), which in the whole-brain analysis were found to activate the PPC. This did not reveal any significant effect, even not in the occipital areas BA17, BA18 and BA19 (where activity was modulated according to distractor salience, cf. Fig. 3-4). This suggests again that salience was processed locally within the occipital cortex, and that the PPC did not intervene for distractor suppression/target enhancement (see also the behavioral effects of salience above, compared to results in Beffara *et al.*, 2022 that did show a different pattern of behavioral and connectivity results, indicative of distractor suppression/target enhancement when endogenous control was more strongly engaged).

3.5 CONCLUSION

We investigated the joint impact of target selection, color-based salience and target statistical spatial regularities on spatial representations along the visual processing hierarchy. We found that all these attention selection signals affected occipital activity in a spatially-specific manner. First, salient distractors’ effects were observed across the visual hierarchy and independently of an interplay with the dorsal frontoparietal network. Secondly, statistical regularities decreased the spatial bias towards the target representation in BA17, and this was independent of parietal-occipital interactions. However, statistical regularities af-

affected the functional connectivity between BA18 and BA19. These results demonstrate that the integration of attentional signals in the occipital cortex rely on both parietal-occipital interactions, as well as local processing within the occipital visual cortex. These findings contribute to the debate concerning how statistical regularities affect processing priorities, here pointing to substantial differences compared to salience processing: while salience was associated primarily with local effects within the occipital cortex, statistical regularities engaged a combination of local occipital processing and occipito-parietal inter-regional interactions.

Chapter 4

Experiment 3 - Interaction between reward-, goal- and salience-related attentional signals in the occipital cortex

Manuscript in preparation

ABSTRACT

Multiple signals contribute to the behavioral relevance of visual information that is selected by attention. Beyond the traditional goal- and salience-related signals, reward-related signals are acknowledged to play a key role in the control of attention, but their possible interaction with other signals is still debated. Here we tested the joint influence of goals, salience and reward on spatially-specific responses in the occipital visual cortex. Behaviorally, targets presented at the high-reward location (HRL) did not significantly affect behavioral performance, but we found that the bias of occipital activity towards the target location was actually reduced when this was presented at the HRL compared to the low-reward location (LRL). Moreover, we found an interaction between goals, reward and salience in the occipital cortex, with the effect of salience being suppressed when salient targets were presented at HRL. Together, these results highlight a significant interdependence between goals, salience and reward that jointly affect spatial representations in the occipital cortex during attentional control. This study highlights new possible mechanisms at play during the control of attention in the presence of multiple attentional signals.

4.1 INTRODUCTION

Visual selective attention prioritizes the processing of behaviorally relevant – over irrelevant – visual information (Desimone & Duncan, 1995; Clark, 2003; Dukas, 2004; Chelazzi, Della Libera, *et al.*, 2011). Behavioral relevance is often accounted for by the correspondence between visual information and the organism’s current goal (task-relevance attentional signal) and by its physical salience (exogenous attentional signal) (Desimone & Duncan, 1995; Corbetta & Shulman, 2002). In real life, visual scenes contain multiple items whose behavioral relevance varies as a function of both their task relevance and their physical salience (Itti & Koch, 2001; Melloni *et al.*, 2012; Macaluso & Doricchi, 2013; Sprague *et al.*, 2018; Beffara *et al.*, 2022). At the brain level, these attentional signals are known to be represented in spatially-organized maps of the visual scene (see “priority maps”; in regions of the dorsal frontoparietal network, see Gottlieb, 2007; Ptak, 2012; Bisley & Mirpour, 2019; in occipital regions, see Melloni *et al.*, 2012; Sprague *et al.*, 2018; Won *et al.*, 2020) where activity increases as a function of both the level of task-relevance and physical salience of the different items in the visual field (Thompson & Bichot, 2005; Melloni *et al.*, 2012; Sprague *et al.*, 2018; Beffara *et al.*, 2022).

More recently, it has been highlighted that task-relevance and physical salience do not fully account for the attentional prioritization (Awh *et al.*, 2012). Several additional classes of signals contribute to attention control, such as statistical regularities (Awh *et al.*, 2012; Ferrante *et al.*, 2018; Won *et al.*, 2020; Adam & Serences, 2021; Zhang *et al.*, 2021) and social factors (Klein *et al.*, 2009), as well as reward (Pessoa, 2010; Anderson, Laurent, *et al.*, 2011; Anderson, 2016; Bourgeois, Chelazzi, *et al.*, 2016). The contribution of reward to attention control has been investigated with behavioral methods (e.g. Anderson, Laurent, *et al.*, 2011; Chelazzi, Estocinova, *et al.*, 2014, see Chelazzi, Perlato, *et al.*, 2013 for a review) and in brain studies (Serences, 2008; Buschsulte *et al.*, 2014; Hickey & Peelen, 2015; Todd & Manaligod, 2018; Shapcott *et al.*, 2020; Grahek *et al.*, 2021; Bourgeois, Sterpenich, *et al.*, 2022). At the behavioral level, the role of reward has been studied using visual search tasks, where participants were trained to associate specific target features (e.g. color in Anderson, Laurent, *et al.*, 2011) or target spatial location (Chelazzi, Estocinova, *et al.*, 2014) with high or low rewards. These studies typically revealed better performance when the target’s spatial location was associated with high reward than low reward, even when rewards are no longer delivered (Chelazzi, Estocinova, *et al.*, 2014), or conversely poorer performances when a distractor was previously associated with a reward feature (Anderson, Laurent, *et al.*, 2011). Reward manipulations in visual search tasks can be considered a special cases of trial history (Awh *et al.*, 2012; Theeuwes, 2018), which can be fully orthogonalized with respect to task-relevance. This is not the case for the manipulations of trial history based on statistical regularities across spatial locations and/or features. For example, varying the amount of reward delivered to the participants when they correctly discriminate a

target at one specific spatial location (e.g. Chelazzi, Estocinova, *et al.*, 2014) does not provide them with any information about where the target is most likely to be presented. On the contrary, statistical regularities across spatial locations and/or features entail a potential contribution/confound of task-relevance: regularities indirectly indicate which spatial locations (Ferrante *et al.*, 2018; Zhang *et al.*, 2021) and/or features (Wolfe *et al.*, 2003; Ferrante *et al.*, 2018; Won *et al.*, 2020; Adam & Serences, 2021; Zhang *et al.*, 2021) are relevant for the task. For example, if the statistical regularities relate to the probabilities of target location on each trial, then knowledge (even implicit) about these probabilities can be exploited to increase task performances (see Ferrante *et al.*, 2018). Moreover, studies that manipulated the regularity of task-irrelevant distractors, often concerned salient distractors (e.g. of a color singleton) (see Melloni *et al.*, 2012; Ferrante *et al.*, 2018; Won *et al.*, 2020; Zhang *et al.*, 2021). Thus, in a task comprising only two possible configurations – one without any salient distractor, and one with a salient distractor (Ferrante *et al.*, 2018; Won *et al.*, 2020; Zhang *et al.*, 2021) – a high distractor presence/location probability allows participants to easily ignore the salient distractor.

In line with this inter-dependence, Won and colleagues (2020) showed that salience and statistical regularities are not processed independently at the brain level. They manipulated the (high vs. low) probability for a salient distractor to be present on each trial. When the distractor-presence probability was low, the occipital spatial representation of the salient distractor was boosted compared to the representation of the non-salient distractors while when distractor-presence probability was high, the occipital representations of both salient and non-salient distractors were similar: that is, when the salient distractor's presence could be anticipated, it was actively suppressed because of its task-irrelevance (Won *et al.*, 2020, and see Zhang *et al.*, 2021 for concordant results on the probabilities of spatial location of the salient distractor). These results account for the complex processing of attentional priorities in the brain that, depending on the task configuration, involve enhancement/suppression mechanisms between the representation of the different items (see Folk *et al.*, 1992; Won *et al.*, 2020; Zhang *et al.*, 2021; Beffara *et al.*, 2022 for works on distractor suppression/target enhancement, and see Geng, 2014; Chelazzi, Marini, *et al.*, 2019; Anderson, 2021; Geng & Duarte, 2021; Luck, Gaspelin, *et al.*, 2021 for reviews), when multiple attentional signals compete in the visual scene.

However, because reward can be manipulated independently of task-relevance and physical salience (see above), how reward is involved in competitive interactions with other attentional signals is unknown, which is crucial to fully comprehend the mechanisms involved in the processing of attentional priorities. For example, in search tasks where a color has been previously associated with a high monetary reward, the presentation of a distractor of this color impedes behavioral performances, when the reward-associated color was never the target (Anderson, Laurent, *et al.*, 2011; Bourgeois, Sterpenich, *et al.*,

2022). In addition, Kim & Anderson (2021) used a search task during which participants first associated a target color with a reward and another with no reward in a training phase. In parallel, during this training phase, Kim & Anderson (2021) manipulated the probability location of a salient distractor, with one specific location being the high distractor probability location. During the test phase, no more reward was delivered, and the colors previously associated with reward/no reward were now used to manipulate both distractor salience and reward. During this test phase, unlike in the training phase, the salient distractor was presented at all spatial locations with equal probability. The results showed that salient distractors presented in the high distractor probability location of the training phase impeded search abilities to a weaker extent compared with salient distractors presented at other locations (i.e. effect of distractor suppression, see Won *et al.*, 2020; Zhang *et al.*, 2021). In addition, when the color of the salient distractor was the one previously associated with a reward, it reduced search abilities regardless of the distractor location. These results indicate that, unlike highly probable salient distractors (Won *et al.*, 2020; Zhang *et al.*, 2021), fully task-irrelevant reward signals may operate independently of other attentional signals (e.g. they are not suppressed). In an EEG study, Grahek and colleagues (2021) investigated the interplay between attention and reward by using steady state visual evoked potentials (SSVEP). The participants were presented with two differently colored superimposed random dot kinematograms (RDK) which flickered at different frequencies. This difference in frequencies elicited distinguishable signatures at the occipital level. On each trial, participants were instructed to attend to one of the two RDK. One color was associated with a high probability of obtaining a reward, while the other was associated with a low probability of reward. This led to a 2 (attended/unattended RDK) x 2 (high/low reward) design. The results showed an effect of attention, with a higher SSVEP amplitude evoked by the attended RDK compared with the unattended one. In addition, Grahek and colleagues (2021) found an effect of reward independently of attention: the SSVEP amplitude was higher when the RDK was associated with high reward probability regardless of whether the RDK was attended or unattended. These results support the idea according to which goal-related and reward-related signals are processed independently.

Kim & Anderson (2021) proposed that this independence may be due to the fact that effects of statistical regularities and reward, albeit eliciting similar behavioral changes, rely on (at least partially) different brain processes. Indeed, attentional control is often found to rely on a distributed frontoparietal network (see Corbetta & Shulman, 2002; Vossel, Geng, *et al.*, 2014) while the processing of reward activates a reward dopaminergic system mostly comprising subcortical structures of the basal ganglia (Pessoa, 2010; Anderson, Laurent, *et al.*, 2014; Pessoa, 2015; Anderson, 2016; Anderson, Kuwabara, *et al.*, 2017). Regarding the influence of reward on attentional control, Anderson and colleagues (2014) used a similar search task paradigm as in Anderson and colleagues

(2011) (cf. above). Using fMRI, they showed that on trials where a distractor stimulus was of the same color as high reward targets in the training phase, activation increased in the tail of the caudate nucleus, in the extrastriate cortex and in the intraparietal sulcus (IPS, a node of the dorsal attentional network). In a similar fMRI study, Bourgeois and colleagues (2022) found that reward-associated distractors activated the frontal eye field (FEF), a node of the dorsal attention-control system, and that they induced an increased connectivity between the FEF and the striatum (a node of the reward system).

While these studies highlight a key role of the reward system in the processing of reward signals during attentional tasks, they also underline a possible interplay between the reward and the attention-control systems (Anderson, 2016; Bourgeois, Sterpenich, *et al.*, 2022). Hence, in contrast with the dominant view positing that reward signals may be processed independently of goal-related signals (Kim & Anderson, 2021), there may actually be some interplay between these two signal-types. For example, in a behavioral study, Preciado and colleagues (2017) showed that goal-related signals can overcome reward signals. In a first experiment, they used a 2-item search task. The first phase of each trial consisted in 2 colored solid discs, one in each screen side. On a portion of the trials only, a specific color (counterbalanced across participants) was used for one of the 2 discs and indicated that a reward was likely to be delivered if the target was presented at this very location and correctly discriminated. It was not predictive of the target location. Behavioral performances were better for targets presented at the same location as this colored-disc than for targets presented on the other screen side. This showed that reward attracted attention. In a second experiment, they made a slight change in the protocol: this time, the reward-colored disc indicated not only that reward was likely to be delivered if the target was correctly detected at that specific location, but also that the target was likely to be presented at the opposite side location. At variance with their first experiment, they found that behavioral performances were higher for targets presented on the opposite side of the reward-colored disc than for targets presented at the reward-colored disc location, which was also the highly rewarded location. In addition, Preciado and colleagues (2017) found that behavioral performances were poorer for targets presented at the reward-congruent location than for targets in neutral trials (when no reward-color was presented during the first phase of the trial). Together, these results show that, when counterproductive for the task at hand, reward signals can be suppressed.

Buschsulte and colleagues (2014) used MEG to investigate the interplay between goals- and reward-related signals at the brain level. The search task comprised 2 bicolor items, presented one on each side of the screen. A total of 5 colors were used. From these colors, one was used as a target-defining feature, another one was used as a reward signal and the 3 remaining ones were control colors. Hence, there were 3 possible trial types: neutral trials (where one item contained the target color plus a control color, and

the other contained 2 control colors), rewarded target trials (where one item contained the target color plus the reward color, and the other contained 2 control colors) and distractor reward trials (where one item contained the target color plus a control color, and the other item contained the reward color plus a control color). The participants' task was to identify the (right/left) side of the target color within the target item. In a first experiment, participants received a low reward for a correct target discrimination on rewarded target trials. Buschsulte and colleagues (2014) found higher event-related magnetic field (ERMF) amplitude in the occipital representation of the non-target item location when it contained the reward color than when it did not. In a second experiment, they increased the amount of reward delivered on rewarded target trials. This abolished the difference of ERMF amplitude found in experiment 1. Buschsulte and colleagues (2014) interpreted these findings as an active suppression of the reward signal when it was likely to interfere with the task at hand. The interplay between goal-directed attention and reward has been studied also using more naturalistic stimuli. In Hickey & Peelen (2015), participants viewed naturalistic scenes in which they had to find a cued object. Correct detection of one of the cued object (e.g. a car) earned high reward, correct detection of some other cued objects earned low reward and some other objects were not associated with any reward (neutral condition). When a "low-reward object" was cued, the visual scene could also contain the "high-reward object". Using MVPA decoding, they found that high-reward objects displayed as target (cued object) increased the occipital representation of this object, compared to neutral condition. On the contrary, high-reward objects displayed as distractors (i.e. when these objects were not the cued objects) elicited lower object representation in the occipital cortex. These findings again suggest possible interplays between task-relevance and reward.

Currently, the ongoing debate about how reward-signals are implemented in priority maps leave the issue of their interaction with other signals unresolved. Here, we tested the joint contributions of reward, goals and salience on the processing of attentional priorities in the occipital cortex and investigated the brain mechanisms underlying the joint processing of these signals. To do so, we had participants performing a 4-item visual search task, where 1 item was presented in each quadrant of the screen. The target was equally likely to be presented in each quadrant (operationalization of goal-directed attention). In order to manipulate reward, one of the 4 quadrants was associated with high reward for a correct discrimination of the target presented in it, while the 3 remaining quadrants were associated with low reward. Independently of the reward manipulation, we manipulated the physical salience using 3 possible display-conditions: all items equally salient (homogeneous display, HD), salient target (salient target display, STD) and salient distractor (salient distractor display, SDD). This resulted in 2 (high/low rewarded target quadrant) x 3 (display-conditions) design. Here, in order to specifically account for the effect of reward on attentional priorities, we calculated spatial bias vectors that indexed to what

extent the activity in the occipital cortex was biased towards the spatial representation of the target. On the basis of the 2 competing views about the implementation of reward in the processing of attentional priorities (cf. above), we hypothesized that if reward was processed fully independently of goals and salience, the spatial bias towards the target quadrant representation would increase for targets presented in in high-reward quadrant, and this increase would be independent of the effect of salience. On the contrary, if reward was dependent on the computation of other signals, we expected that the 3 signals would affect the spatial bias vector in a non linear manner. This could, for example, involve a reduction of spatial bias towards the target quadrant for targets presented in the high reward quadrant, and/or a reduction of the effect of salience on the bias vector when a target presented in the high-reward quadrant is also salient (i.e., reward-related salience suppression).

4.2 MATERIAL & METHODS

4.2.1 Participants

We recruited 23 right-handed healthy adults for this study. They had normal or corrected-to-normal vision, no neurological, psychiatric or cognitive impairments and gave their written informed consent to participate in the study. The study was approved by a national ethics committee in biomedical research (Comité de Protection des Personnes: Sud-Méditerranée II, authorization ID: 2019-A00713-54). 17 participants were included in the final analyses (mean age: 23, range 20-29; 8 females). 6 participants were excluded because they moved the eyes towards the stimuli locations during the main attentional task (preventing us from obtaining stable quadrant-specific occipital responses) and/or did not perform the task accurately enough (preventing us from constructing predictors for at least one experimental condition).

4.2.2 Experimental design

The experiment consisted of 5 functional imaging runs, with 4 runs of the main attention task (12 min each) plus 1 localizer run (10 min) and one anatomical scan (6 min). The visual stimuli were presented using Cogent Graphics, developed by John Romaya at the Wellcome Department of Imaging Neuroscience, running under MATLAB (The MathWorks, Natick, MA) and were projected on a screen placed at 90cm from the participant's eyes (1024 x 768 pixels; projected image size: 31.5cm height x 42cm width).

Localizer task

The localizer task was used to identify and select the occipital representations of each 4 quadrants of the screen (TL, top-left; TR, top-right; BR, bottom-right or BL, bottom-left locations), where the visual stimuli of the main attentional task were displayed (see

next section). To do so, we presented visual stimuli consisting in a moving ($28^\circ/\text{sec}$) array of small bars (approximately 9 bars at a time, $0.5 \times 0.1^\circ$ each) in a square aperture ($3 \times 3^\circ$) in one of the 4 screen quadrants on each stimulation block. All bars were oriented horizontally or vertically, but the to-be-detected target-bars that were 45° left/right tilted from vertical. The targets were presented at unpredictable times in the quadrant aperture (range 1.08-3.24sec). While they maintained eye fixation at the center of the screen during the whole blocked stimulation, participants had to judge the targets' left/right tilt by pressing a response-button with the index/middle finger of the right hand. For each block, the stimuli were presented in the screen quadrant for 14 seconds, interleaved with 12 seconds of central fixation without any visual stimulation. Each quadrant was stimulated 6 times, in a randomized order, see also Beffara *et al.*, 2022.

Main attentional task

There were 4 fMRI-runs of the main attentional task. Each run comprised 72 trials. Each trial started with a 1000ms preparatory phase where a central fixation dot (0.5° diameter) was displayed in a light grey color indicating the imminent presentation of the stimulation array. The stimulation array comprised 4 oriented bars (eccentricity = 7° , size = $2.0 \times 0.5^\circ$ each), one in each screen quadrant and lasted for 300ms. The target bar was tilted -25° or 25° from the vertical, while the 3 distractor bars were tilted -25° or 25° from the horizontal. A dot was placed either in the top or the bottom part of each bar. The participants' goal was to indicate the up/down location of the dot placed inside the target bar by pressing a response-button with the index/middle finger of the right hand, while maintaining fixation at the center of the screen. The 3 distractor bars were fully irrelevant for the task at hand. Participants could give a keypress during a response time-window of 3000ms after the stimulation array onset.

On each trial, the array could either comprise 4 bars of the same color (green or red, counterbalanced across participants) or include a color singleton (one green bar among three red bars, or vice-versa). This constituted the 3 display-conditions that were used to operationalize the manipulation of stimulus-driven salience: Homogeneous Display (HD, all stimuli of the same color), Salient Target Display (STD, when the target was the color singleton) and Salient Distractor Display (SDD, when the distractor stimulus in the quadrant opposite the target was the color singleton). In order to reduce the total number of possible conditions, in the SDD condition the salient distractor always appeared in the quadrant opposite to the target quadrant. The three display-conditions were presented with equal probability (1/3 chance each).

To operationalize the reward attentional signal, and independently of the display-conditions, we manipulated the amount of reward distributed on each trial. A "high-rewarded location" (HRL), one of the 4 quadrants, was randomly assigned to each

participant. Across all the 4 runs, a correct judgement of the target bar presented at the HRL was rewarded 100 points with 83% probability and 1 point with 17% probability, while a correct judgement of the target presented at one of the 3 remaining “low-rewarded locations” (LRL) was rewarded 1 point with 83% probability and 100 points with 17% probability. Incorrect responses were not rewarded. To avoid speed/accuracy trade-off, reward was not delivered (+0) for response times (RTs) longer than 1000ms. For these trials, participants were informed that they had been too slow. The inter-trial interval was between 3000 and 4000ms (uniform distribution) and was followed by a 1000ms reward phase indicating both the amount of reward distributed on the current trial (+0/+1/+100) and the total amount of points accumulated during the current run. Participants were told that they would be offered sugary goodies at the end of the experiment as a function of their total amount of cumulated points across the 4 experimental runs. The inter-trial interval was between 3000 and 5000ms (uniform distribution).

The combination of display-conditions and reward-location resulted in a fully-factorial design: 3 display-conditions (HD, STD, SDD) x 2 target-probability location (HRL, LRL) x 4 target locations (i.e. the screen quadrants: TL, TR, BR, BL).

4.2.3 Eye tracking

Gaze-position was recorded throughout the whole experiment using a MR-compatible EyeLink 1000 (SR Research Ltd., Mississauga, Ontario, Canada) at a sampling rate of 500Hz. Calibration was performed using the four screen quadrants where the visual stimuli were presented during the main attentional task (7° eccentricity), plus the screen center. Eye-tracking data analysis was performed using custom MATLAB scripts. We first extracted data in a 2500ms window starting 500ms before the preparatory phase onset for each trial. We used the first 500ms of this time-window to baseline-adjust data using the median of the vertical and horizontal eye-position. Then, we assessed the quality of each trial’s data considering the percentage of data-points larger than 10°/smaller than -10°, caused by eye blinks or noisy signal. We only selected trials with less than 50% of these unreliable data-points (97% of the trials) for further analyses. In these trials, displacements of the gaze-position larger than 0.5° and lasting for at least 100ms were classified as an eye-saccade. Trials comprising at least 1 eye-saccade outside a central box of 2° from the center of the screen (2% of the trials with reliable data) were excluded from behavioral analyses and modeled in a dedicated regressor of non-interest in the imaging analyses.

4.2.4 Behavioral analyses

At the end of the experiment, participants were asked i) whether they noticed anything particular during the experiment, ii) whether they noticed any pattern of reward location

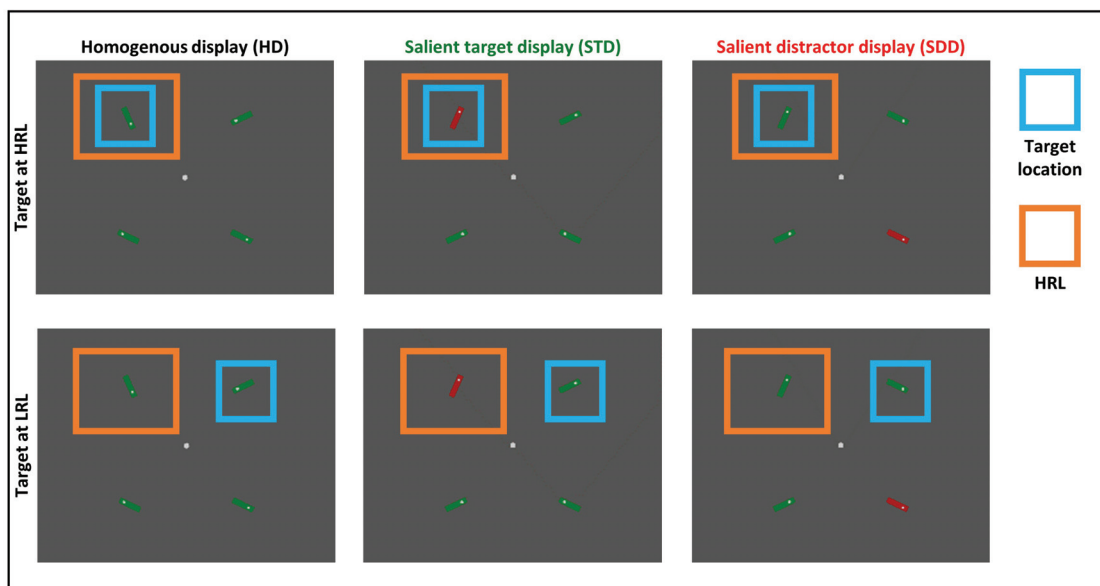


Figure 4.1: **Figure 1. The 2 (reward-locations) x 3 (display-conditions) main experimental conditions.**

The example shows that, for a target appearing in one specific screen quadrant (here top-left, in the blue square for illustration purpose), there were 6 possible experimental conditions. The 6 main experimental conditions correspond to a 2 (reward-locations) x 3 (display-conditions) design. The stimulus-driven salience was operationalized using a color singleton item: the 4 stimuli could be of the same color (HD condition), the target could be the color singleton (STD condition) or the distractor opposite to the target quadrant could be the color singleton (SDD). These 3 display-conditions were presented in 2 distinct reward-locations conditions: either the target appeared in the “high reward quadrant” (HRL; the orange square here, for illustration purpose; see top panels), or in the “low reward quadrant” (LRL; see bottom panels).

during the experiment, iii) to guess what was the HRL.

We analyzed the RTs and accuracy data for the main attentional task using linear mixed models implemented in R-studio (Bates *et al.*, 2015). For the RTs analysis, we excluded trials for which participants provided wrong, late, or no keypress response and/or did not maintain central eye fixation (cf. above). The model included the log-transformed RTs as the dependent variable and the display-condition (with 3 levels: HD, STD, SDD), the reward-location condition (with 2 levels: HRL, LRL) and their interaction as the explanatory variables. For the accuracy analysis, only trials including losses of fixation were discarded from the analysis. The model included the response validity (right or wrong) modeled using a binomial law as the dependent variable, and the display-condition, the reward-location and their interaction as explanatory variables. Because of the repeated measures, both models also included subject-specific intercepts.

4.2.5 Image acquisition and preprocessing

T2*-weighted echoplanar images (EPI) with blood oxygen level-dependent (BOLD) contrast (interleaved multiband sequence, Multiband Factor = 2, 50 slices covering the entire brain, field of view = 220x210.4mm, Repetition Time = 1.72s, echo time = 30ms, phase encoding direction = antero-posterior, slice orientation = approx. axial, voxel size = 2.4 x 2.4 x 2.4mm³) were obtained using a 3T MRI System (Trio, Siemens). A high-resolution anatomical scan was acquired using a standard T1-weighted 3D MP-RAGE sequence (Repetition Time = 3s, echo time = 3.8ms, voxel size = 1 x 1 x 1mm³).

The functional data were preprocessed and analyzed with Statistical Parametric Mapping software SPM12 (Wellcome Department of Imaging Neuroscience, University College London, UK; <http://www.fil.ion.ucl.ac.uk/spm>). After discarding the first four volumes of each imaging run, images were corrected for head movements. Slice-acquisition delays were corrected using the middle slice as reference. All images were normalized to the SPM12 Tissue Probability Map and re-sampled to 2mm isotropic voxel size. Unsmoothed data were used for ROI analyses and smoothed data were used for whole-brain and psychophysiological interactions analyses.

4.2.6 Single-subject analyses

Localizer and individual Regions Of Interest (ROIs)

The procedure for the ROIs definition conducted in the current study is detailed in Befara and colleagues (2022). The localizer single-subject model (GLM) comprised the 4 conditions corresponding to the 4 screen quadrants where the localizer stimuli could be presented (i.e. TL, TR, BR, BL locations, blocks of 14 seconds), plus the 6 movements parameters included as regressors of non-interest. These were convolved using the SPM12 “Haemodynamic Response Function”. First, for each participant, at the whole-brain level, we tested the main effects of the side of the screen quadrant where the localizer stimuli were presented (e.g. "TL+BL > TR+BR", for left hemifield quadrants) and separated voxels responding to stimuli in the upper or the lower quadrant by using inclusive masking with the relevant effect of top/bottom stimulation (i.e. top-left quadrant: "TL > BL", and bottom-left quadrant: "BL>TL"). All contrasts were thresholded at p-uncorrected = 0.005. Secondly, the subject- and quadrant-specific responses were split based on the Automated Anatomical Labeling atlas (AAL, Tzourio-Mazoyer *et al.*, 2002) to define ROIs on the basis of both quadrant-specificity and anatomically-defined occipital Brodmann areas BA17, BA18 and BA19. This resulted in a total of 12 ROIs per participant (i.e. 3 BA: BA17, BA18, BA19 x 4 quadrants: TL, TR, BR, BL). The average size of the quadrant-specific ROIs (mean number of voxels \pm SEM) was: 105.15 \pm 0.99 for BA17, 242.15 \pm 1.34 for BA18 and 215.32 \pm 1.56 for BA19.

Main task

The main attentional task was analyzed using two separate single-subject GLMs. The first one aimed at investigating quadrant-specific responses in the occipital visual cortex (cf. subject-specific ROI analyses), while the second aimed at testing the overall effects of salience and reward at the whole-brain level and irrespective of target-quadrant.

In order to study the quadrant-specific responses, the first GLM comprised 12 conditions of interest: 1 HRL quadrant x 3 display-conditions (HD, STD, SDD) + 3 LRL quadrants x 3 display-conditions, plus one predictor including all trials to be excluded (no response, incorrect orientation-discrimination, reaction time out of the response window and fixation-loss trials) and the 6 movement parameters. The amount of reward delivered on each trial was modeled by entering 3 additional regressors corresponding to the 3 possible reward amounts (+0/+1/+100). Each trial was modeled using the canonical Hemodynamic Response Function in SPM12. For the 12 main conditions, the event-onsets were time locked to the presentation of the stimulus display and the event-duration was 300ms. The 3 reward-delivery conditions were time locked to the reward phase onset, with an event-duration of 1000ms. Only the parameter estimates of the 12 conditions of interest were used for the subsequent group-level analyses.

The second single-subject GLM comprised 9 conditions of interest: 2 reward-locations (HRL, LRL) x 3 display-conditions (HD, STD, SDD), the 3 possible reward amounts delivered on each trial, plus one predictor including trials to be excluded from the group analyses and the 6 movement parameters. Each trial was modeled using the canonical Hemodynamic Response Function in SPM12. The 2x3 main conditions were time locked to the presentation of the stimulus display (duration = 300ms), while the 3 reward-delivery conditions were time locked to the reward phase onset (duration = 1000ms). The parameter estimates of the 6 main conditions were used for the subsequent group-level analyses of reward-location and display-condition. In a separate analysis, the parameter estimates of the 3 reward-delivery were used for the group-level analyses of the reward amount effect on whole-brain responses.

4.2.7 Group-level analyses of spatially-specific occipital responses

Target selection, display-conditions and reward-locations

Our primary interest was to assess the shaping of the spatially-specific occipital responses by reward-location and display-conditions, see Beffara *et al.*, 2022. First, we examined the activity in the ROIs representing the target-quadrant and the opposite quadrant, as a function of the type(s) of priority signals present in these two quadrants. We averaged the response estimates in the occipital ROIs (separately for BA17, BA18 and BA19), considering whether the represented quadrant included the location of the target ("ROI_IN")

or the location opposite to the target ("ROI_OPP", where the salient distractor was presented in the SDD condition). This was done separately for the 3 display-conditions (HD, STD, SDD) and according to whether the target-quadrant was also the high reward-location (HRL) or not (LRL), that constituted the 6 conditions of interest. This resulted in a single average value per subject for each ROI-type (IN/OPP), BA and experimental condition (3 displays x 2 reward-locations). A 2x2x3x3 repeated-measure ANOVA with the factors: quadrant-type (ROI_IN, ROI_OPP) x reward-location (HRL, LRL) x display-condition (HD, STD, SDD) x BA (BA17, BA18, B19) was employed to assess these effects.

Spatial bias vectors

Next, we examined how target, salience and reward-location jointly affected the overall 2D representation of visual space, now considering also the activity in the ROI representing the quadrant ipsilateral to the target quadrant ("ROI_IPSI", same hemifield as the target, but different up/down location) and the contralateral quadrant ("ROI_CONTRA", opposite hemifield, but same up/down location as the target), please see Beffara *et al.*, 2022 for a detailed explanation and graphical illustrations of these analyses. Briefly, separately for each subject and BA-area, the activity of 4 ROIs representing the 4 quadrants was used to construct a vector that represents the direction and magnitude of the spatial bias coded by the BA-area. Here these vectors were constructed separately for the 3 display-conditions and the 2 reward-locations conditions. The data analyses considered the measure of the distance between the subject-specific vector coordinates (X,Y) and a virtual coordinate representing a spatial bias exactly pointing towards the target-quadrant representation (ROI_IN, 45° from left horizontal axis, see dotted lines on Fig. 4 top panels). We chose (-70; 70) as this virtual coordinate, because 70 was the maximum absolute value of all X and Y coordinates irrespective of the reward-location, display-condition and BA. Hence, any increase of distance between these virtual coordinates and the subject-specific datapoints expressed a decrease of spatial bias towards the target-quadrant ROI_IN (decrease of vector magnitude and/or direction, see Fig. 4). The distance was calculated as the Euclidian distance: $\sqrt{(-70 - X)^2 + (70 - Y)^2}$. The effects of reward and display-conditions were tested using repeated-measures ANOVAs and pairwise paired t-tests.

Whole-brain activations

Beside the modulation of the activity in occipital regions that represents the different visual quadrants (cf. section above), we also examined the effect of reward and display-conditions at the whole brain level, now irrespective of the specific location where the target was presented (see also Bourgeois, Sterpenich, *et al.*, 2022). The 6 contrast images resulting from the second set of single-subject GLMs (2 reward-locations x 3 display-conditions, see above) were entered in a group-level repeated-measures ANOVA.

We then performed the relevant T-contrasts to highlight activations corresponding to both types of priority signals (reward: HRL > LRL and LRL > HRL; physical salience: STD > HD, SDD > HD, SDD > STD and STD > SDD). Significant activations reported here were thresholded at p-FWE-corrected = 0.05 at the cluster level, with the cluster-sizes defined at a voxel-wise threshold of p-uncorrected = 0.005, considering the whole brain as the volume of interest. Results are visualized using SPM and MRICro.

To assess the direct effect of the reward amount at the whole-brain level, we performed group-level repeated-measures analyses using the 3 contrast-images corresponding to the 3 reward amounts conditions from the subject-level analyses. We performed the relevant T-contrasts to highlight activations corresponding to varying reward amounts (+100 > +1, +100 > +0, +1 > +0, +0 > +1, +0 > +100, +1 > +100).

4.3 MATERIAL & METHODS

4.3.1 Behavioral data

None of the participants noticed something particular or any reward unbalance of reward across quadrants. When forced to guess, 5/16 participants were able to report which quadrant was the HRL.

We measured RTs and accuracy in the 6 main experimental conditions to assess the behavioral effect of both reward-locations and display-conditions. Analysis of the RTs showed a significant main effect of display-conditions, with participants being faster for STD than for HD, and for HD than for SDD ($F(2,4153) = 134.66$, $p < 0.001$; HD, $685 \pm 4.29\text{ms}$; STD, $635 \pm 3.61\text{ms}$; SDD, $734 \pm 4.95\text{ms}$; fixed-effect Cohen's d for the STD vs. SDD comparison = 0.67) but, unlike previous behavioral studies (Chelazzi, Estocinova, *et al.*, 2014, see also Anderson, Laurent, *et al.*, 2011), we found no significant effect of reward-locations ($F(1,4153) = 0.86$, $p = 0.35$; HRL, $688 \pm 5.18\text{ms}$; LRL, $682 \pm 2.93\text{ms}$) and no significant display-condition x reward-location interaction ($F(2,4153) = 0.09$, $p = 0.91$). Accuracy results followed the same pattern of results as RTs: a significant main effect of the display-conditions, with accuracies in STD > in HD > in SDD ($\chi^2(2,4683) = 42.09$, $p = 0.001$; accuracy for: HD, $87 \pm 1.9\%$; STD, $92 \pm 1.5\%$; SDD, $86 \pm 1.9\%$; fixed-effect odds-ratio for STD vs. SDD = 1.95), but no significant main effect of the reward-locations ($\chi^2(2,4683) = 2.33$, $p = 0.13$; HRL, $88 \pm 1.7\%$; LRL, $89 \pm 1.3\%$) or reward-location x display-condition interaction ($\chi^2(2,4683) = 5.20$, $p = 0.07$). These results show that salient targets are easier to find, while salient distractors impede target discrimination (see also Melloni *et al.*, 2012; Ferrante *et al.*, 2018) and that, surprisingly, targets presented at spatial locations associated with higher reward do not facilitate search abilities under the current experimental conditions (see also Buschsulte *et al.*, 2014 for similar results).

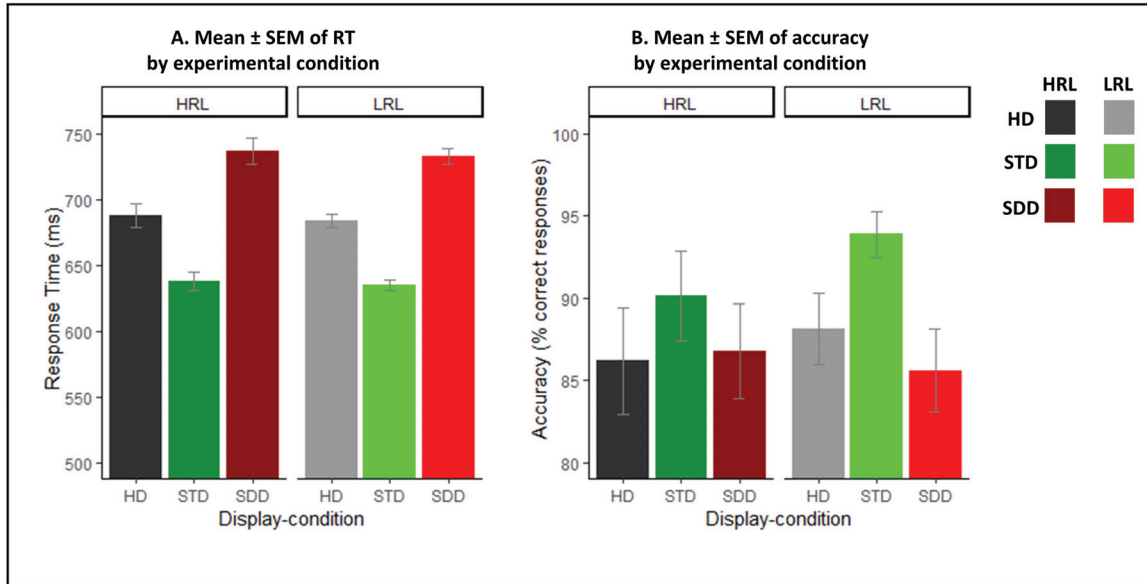


Figure 4.2: **Figure 2. Behavioral performances as a function of the 6 main experimental conditions.**

A - The RTs (mean \pm SEM) showed a significant effect of display-condition (STD < HD < SDD) but no significant effect of reward. **B** - The accuracy data (mean \pm SEM) showed an analogous pattern of results, with a significant effect of display-condition only.

4.3.2 Reward-locations and display-conditions modulate activity in the occipital cortex

Regions representing the target (ROI_IN) and the opposite quadrant (ROI_OPP)

We first aimed at studying how reward and salience attentional signals present in the visual display modulate the quadrant-specific spatial representations across the visual hierarchy. For this, we considered the activity of the occipital region representing the current target location (ROI_IN) and the occipital region representing the opposite quadrant, where the salient distractors were presented in the SDD condition (ROI_OPP). The corresponding 2x3x2x3 ANOVA (ROI_IN/ROI_OPP x display-condition x reward x BA) yielded a significant main effect of ROI-type ($F(2,602) = 25.39$, $p < 0.001$, $\eta^2p = 0.04$; higher activity in ROI_IN than in ROI_OPP, compare Fig. 3 top-panels “ROI_IN” to bottom-panels “ROI”), corresponding to the effect of target selection, a main effect of BA ($F(2,602) = 143.37$, $p < 0.001$, $\eta^2p = 0.34$) and a significant reward x BA interaction ($F(2,602) = 3.12$, $p = 0.045$, $\eta^2p = 0.01$). All other main effects or interactions were not significant ($p > 0.11$). We further investigated the reward x BA effect by performing the pairwise comparisons between HRL and LRL conditions separately for the 3 BAs, but none of these tests reached statistical significance (all $p > 0.18$). These results suggest that only target selection robustly modulated the local activity in the occipital cortex, while reward-location had a minor effect that could not be confirmed at the level of one specific BA.

However, it should be noted that this analysis considered the activity modulation of only 2 spatially-specific occipital ROIs for each BA, and thus cannot account for the overall spatial bias taking place in the occipital cortex and its potential modulation by multiple attentional signals.

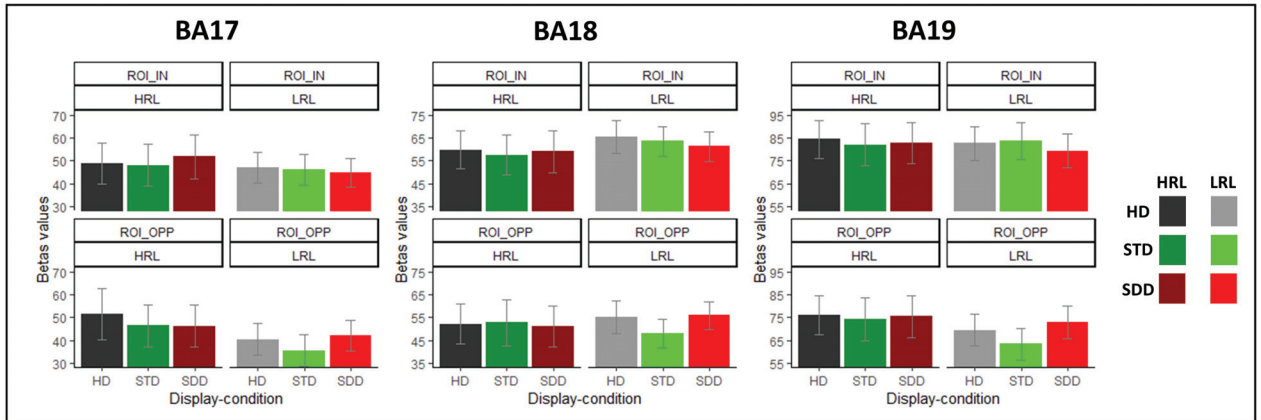


Figure 4.3: **Figure 3. Local responses in ROI_IN and ROI_OPP as a function of display-conditions and reward-locations.**

Left panel shows responses in BA17, middle panel shows responses in BA18 and right panel shows responses in BA19. Grey colors are used for responses in HD, green colors for STD and red colors for SDD. Darker colors are for HRL, brighter colors are for LRL.

Modulation of 2D occipital spatial representations: spatial bias vector analysis

The previous analysis, considering only ROI_IN and ROI_OPP, did not show any clear modulation of the local occipital activity as a function of display-conditions and reward-locations. However, reward and salience are known to modulate attentional priorities (see Awh *et al.*, 2012; Beffara *et al.*, 2022), which may be reflected in the overall spatially-specific activity of the occipital cortex (Beffara *et al.*, 2022). Accordingly, we considered the activity in the 4 ROIs (ROI_IN, ROI_OPP, ROI_IPSI, ROI_CONTRA) of each BA) to compute spatial bias vectors. We considered a 3x2x3 ANOVAs with the factors display-condition x reward-location x BA as the explanatory variables and the distance from virtual coordinates representing a spatial bias exactly oriented towards the target-quadrant representation (cf. Methods).

We found a significant main effect of display-condition ($F(2,298) = 3.39$, $p = 0.035$, $\eta^2p = 0.02$; compare Fig. 4 top-panels green and red vectors magnitude/direction, and Fig. 4 bottom-panels green and red bars), a significant main effect of reward-locations with lower spatial bias in HRL compared to LRL ($F(1,298) = 23.57$, $p < 0.001$; $\eta^2p = 0.09$; compare Fig. 4 top-panels dark- and bright-colored vectors on Fig. 4 top-panels, and dark and bright bars on Fig. 4 bottom-panels), a significant effect of BA ($F(2,298) = 5.84$, $p = 0.003$; $\eta^2p = 0.04$), as well as a significant reward-location x display-condition interaction ($F(2,298) = 6.72$, $p = 0.001$; $\eta^2p = 0.05$). We further investigated this interaction effect

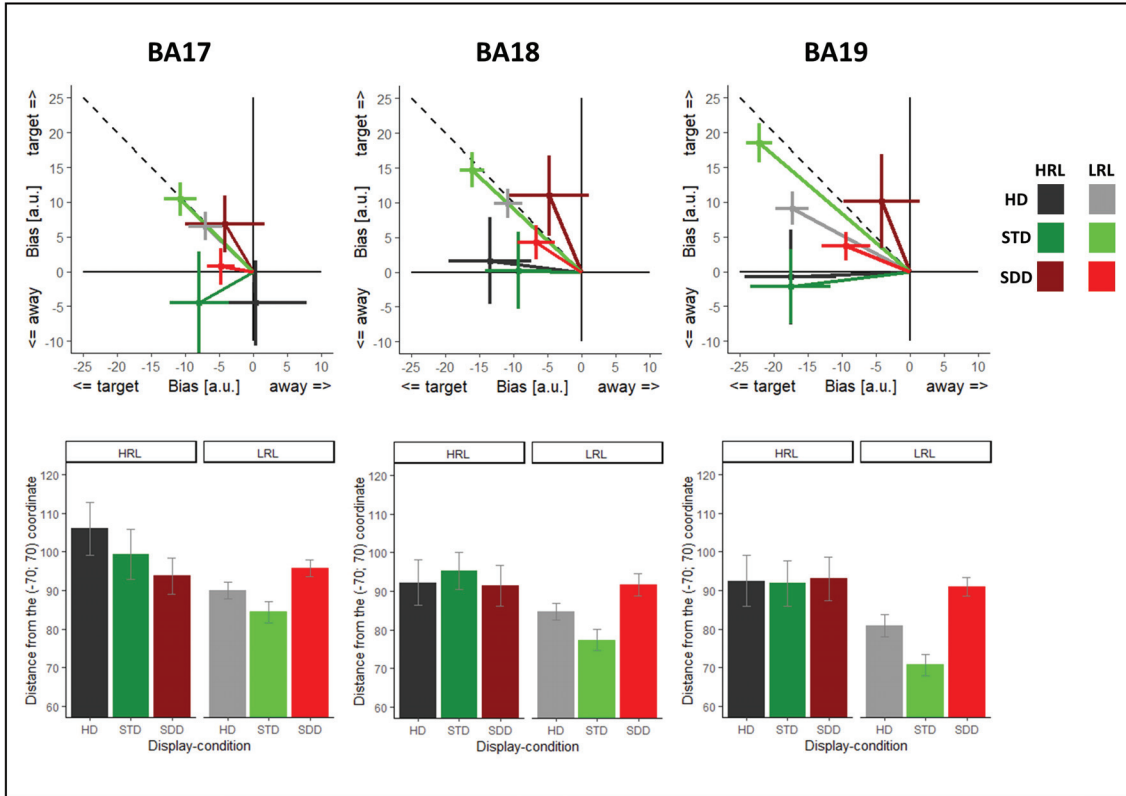


Figure 4.4: **Figure 4. Spatial bias vectors as a function of the reward-locations and display-conditions.**

Top panels show spatial bias vectors in BA17, BA18 and BA19 (left to right). The 45° dotted line represents the direction of the target-quadrant representation, in the arbitrary frame of reference of the bias vectors. Bottom panels show mean distance (+/- SEM) between the virtual representation of the target (-70; 70) and the subject-specific spatial bias vectors for the 2 reward-locations and the 3 display-conditions. Black color is used for vectors in HD, green color for STD and red color for SDD. Darker color vectors are vectors in HRL condition and brighter color vectors are vectors in LRL condition.

by performing the pairwise t-tests between all display-conditions in the 2 reward-location conditions. Only a significant difference was found when comparing STD_{LRL} to SDD_{LRL} : the mean distance from the (-70; 70) coordinate was shorter for STD_{LRL} than for SDD_{LRL} (compare bright-green with bright-red vectors on Fig. 4 top-panels, and bright-green with bright-red bars on Fig. 4 bottom-panels; see Table 1 for related statistics), which shows that the effect of display-condition was only present in LRL, i.e. when the target was presented at low-rewarded locations. In HRL, the vectors had comparable magnitudes than in LRL (compared dark and bright vectors on Fig. 4), but their direction was not specific to the target quadrant representation (cf. dark-colored vectors on Fig. 4, that are further away from the dotted line compared to bright vectors), indicating a loss of spatial specificity when targets were presented at HRL. These results first show that reward-location and display-conditions factors interact, and suggest that reward- and salience-related priorities are not computed independently. In addition, the reduced spatial bias towards the target (compared bright- and dark- colored vectors on Fig. 4)

quadrant in HRL compared to LRL suggests that the task-irrelevant reward signal was overcome by goal signals in this experiment.

Comparison	t-value	p-value
HD _{HRL} versus STD _{HRL}	0.42	1
HD _{HRL} versus SDD _{HRL}	1.19	0.84
STD _{HRL} versus SDD _{HRL}	0.77	0.97
HD _{LRL} versus STD _{LRL}	2.18	0.25
HD _{LRL} versus SDD _{LRL}	-2.15	0.27
STD _{LRL} versus SDD _{LRL}	-4.33	< 0.001

Figure 4.5: **Table 1. Statistics of the pairwise comparisons between display-conditions in both reward-location conditions**

4.3.3 Whole-brain analyses

The reward-based attentional bias is acknowledged to depend on the activity of the reward system (e.g. see Anderson, Laurent, *et al.*, 2014; Anderson, 2016; Anderson, Kuwabara, *et al.*, 2017) but has recently been shown to also involve the dorsal frontoparietal attention control network, particularly the FEF (Bourgeois, Sterpenich, *et al.*, 2022). Accordingly, here we performed a whole-brain group analysis using a 2x3 (reward-location x display-condition) ANOVA and the subsequent relevant t-contrasts (HRL > LRL, LRL > HRL, STD > SDD, SDD > STD). The SDD > STD t-contrast revealed increased activity in the left superior frontal sulcus (MNI coordinates: x = -24, y = 0, z = 58, p-FWE-corrected = 0.03, t = 3.89). All other pairwise comparisons yielded no significant differential activations.

In a separate whole-brain analysis we considered the reward delivery phase and directly compared the effect of the amount of reward delivered on each trial. In particular, we aimed at controlling that our reward manipulation effectively activated the participants' reward system during the task, which we predicted to be more activated when high-reward (100 points for a correct target discrimination) was delivered compared to low-reward (1 point for a correct target discrimination). The "Reward 100 > 1" t-contrast revealed significantly higher responses in the bilateral caudate nucleus (left, MNI coordinates: x = -16, y = -22, z = 24, p-FWE-corrected < 0.001, t = 5.87; right, x = 22, y = -40, z = 14, p-FWE-corrected < 0.001, t = 6.22) as well as in the left superior frontal gyrus (x = 8, y = -24, z = 76, p-FWE-corrected < 0.001, t = 4.76).

These results suggest that the manipulation of salience modulated regions of the dorsal frontoparietal attention control network (left superior frontal sulcus, see above), while the manipulation of reward did not, suggesting that the reward modulation of the occipital spatial bias rely on local competition mechanisms at the occipital level.

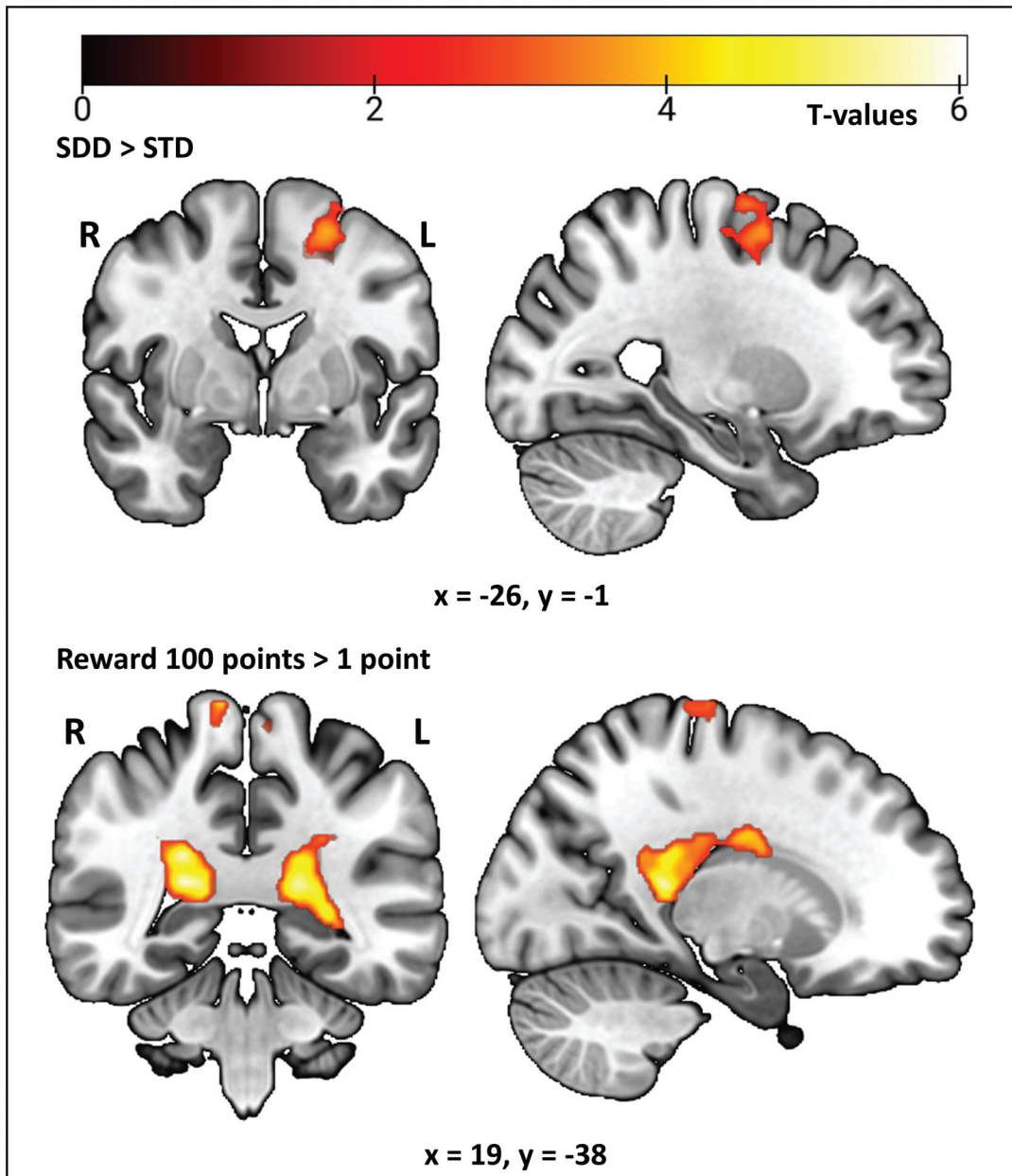


Figure 4.6: **Figure 5. Whole-brain differential responses to SDD minus STD and to high (100 points) minus low (1 point) rewards. Only significant clusters are shown.**

Top panel shows significantly stronger responses to SDD than STD, that are located in the left superior frontal sulcus. Bottom panel shows stronger responses to high rewards delivered during the reward phase compared to low rewards. Stronger responses for high rewards are located along the bilateral caudate nucleus as well as in the superior frontal gyrus.

4.4 DISCUSSION

This study investigated how the joint manipulation of goals, reward and salience signals modulate the activity of spatial representations in the occipital cortex. To do so, we used a visual search task that comprised four items, presented one in each of the 4 screen quadrants. We manipulated independently the reward-value associated with the 4 spa-

tial locations and the salience of the item presented in each quadrant. In addition, we performed whole-brain analyses in order to assess the pattern of responses in the frontoparietal attention control network and the reward system. Behaviorally, we found that salient targets increased, while salient distractors reduced, search performances. No significant effect of reward on behavioral performances was found. We showed that goals, reward and salience induced changes in the spatial pattern of activity in the occipital cortex across the visual hierarchy. In particular, in the current search conditions, targets at the high-reward location were associated with a reduced spatial bias towards this spatial location compared to targets presented at low-reward locations. Whole-brain analyses showed that salience affected responses in the dorsal premotor cortex, while targets presented at high vs. low reward location did not modulate any area of the frontoparietal and reward systems. However, during the reward phase, earning 100 vs. 1 points increased activity in the caudate nucleus (see Anderson, Laurent, *et al.*, 2014). These results suggest that reward-based attentional signals can reduce the attribution of attentional priorities in the occipital cortex. Moreover, as the reduced spatial bias was not associated with any functional changes in regions of the frontoparietal network or the reward system, we suggest that the reward bias was implemented via local competitive interactions at the occipital level, possibly due to proactive suppressive mechanisms of the high-reward location (cf. Geng & Duarte, 2021).

4.4.1 Effects of reward and visual salience on behavioral performance

Previous studies that focused on the effect of visual salience on behavioral performance showed that salient targets increased search performance (e.g. Melloni *et al.*, 2012), while salient distractors hindered performance (e.g. Melloni *et al.*, 2012; Ferrante *et al.*, 2018; Won *et al.*, 2020; Adam & Serences, 2021; Zhang *et al.*, 2021). Here, we replicated these findings, with lower RTs and higher accuracy when the target was salient, and conversely higher RTs and lower accuracy when the distractor was salient. Effects similar to the ones described for salience have also been described for reward, with features (Anderson, Laurent, *et al.*, 2011) and spatial locations (Chelazzi, Estocinova, *et al.*, 2014) associated with high reward leading to better search performances than the ones associated with low reward. Here, we did not replicate these findings, and found no significant effect of reward on behavioral performances.

A possible reason for the discrepancy between the current results and previous work is the way reward is operationalized in visual task and how it is included in the task instructions given to the participants. For example, monetary rewards are often used to motivate participants (Anderson, Laurent, *et al.*, 2011; Chelazzi, Estocinova, *et al.*, 2014, see also Chelazzi, Perlato, *et al.*, 2013), which was not the case here. In addition, here, the points delivered on each trial, which were used to operationalize reward, also contributed

to the overall goal of participants, i.e. to earn a maximum of points. This may have led to some interference between the reward signals (concerning the points to earn throughout the study) and the goal signals (concerning the discrimination of the target on each trial), increasing the competition between the two signal-types. Indeed, Preciado and colleagues (2017) investigated the effect of conflict between goal- and reward-related signals (cf. Introduction). They found that when a reward-associated cue was presented on a given side of screen, and actually indicated that the target was highly likely to be presented on the opposite side, behavioral performance was the highest for targets presented at the side opposite to the reward-cue and was the poorest for targets presented at the reward-cue location. A second reason that may explain the different impact of reward across studies (i.e. attentional capture by the reward item/location in Anderson, Laurent, *et al.*, 2011; Anderson, Laurent, *et al.*, 2014; Buschsulte *et al.*, 2014; Chelazzi, Estocinova, *et al.*, 2014; Preciado *et al.*, 2017; Grahek *et al.*, 2021 vs. suppression in Buschsulte *et al.*, 2014 when the reward signal was associated with the target, Preciado *et al.*, 2017 when combining goal-relevance and reward-associated cue; see Introduction and see also Grahek *et al.*, 2021 during the training phase) may be the strength of the reward signal itself. In Anderson and colleagues (2011; 2014) and Chelazzi and colleagues (2014), they first associated reward with a specific feature/location and focused their main behavioral analyses on a subsequent testing phase when participants knew that no more reward would be delivered. With this configuration, we suggest that the reward-association was effective, but less powerful than in the training where reward was delivered on each trial. On the contrary, in Buschsulte and colleagues (2014), Preciado and colleagues (2017) and in the current study, there was no distinction between association and test phases, which may have led to a potentially strong attentional capture by the reward signal (i.e. reward was delivered in the testing phase), and thus requiring the need to counteract this effect to effectively carry out the target discrimination, even on trials with targets presented at a low-reward location. Accordingly, we suggest that reward-related signals can be counteracted when they are potentially incongruent with goal signals.

4.4.2 Reward signal suppression in the occipital cortex

It is acknowledged that reward signals can capture attention (Chelazzi, Perlato, *et al.*, 2013) and that they can affect activity in the visual cortex (Anderson, Laurent, *et al.*, 2014; Buschsulte *et al.*, 2014; Hickey & Peelen, 2015; Anderson, 2016; Grahek *et al.*, 2021). However, the various operationalization of reward in these experiments yielded conflicting results, often related to how reward affected behavioral response times (see also section above). For example, when reward boosted behavioral performance, reward-associated stimuli boosted occipital representations compared to neutral stimuli (see Grahek *et al.*, 2021), while when reward did not boost response times, reward-associated stimuli reduced occipital responses (see Buschsulte *et al.*, 2014). The relationship between the behavioral effect of reward and activations at the occipital level have also

been investigated by Hickey & Peelen (2015) (cf. Introduction), who tested the effect of reward-associated distractors on both RT-costs and stimulus occipital representation. They found that the more the presence of the reward-associated distractor induced RT-costs, the less it was suppressed at the occipital level. This suggests that reward-signal suppression may directly decrease the attentional capture towards the reward-associated stimuli.

Here, our results showed a decreased spatial bias towards the target quadrant representation when the target was presented at the HRL than when it was presented at the LRL, which can suggest that also targets associated with high reward can lead to a decreased bias towards its representation at the occipital level. Together with the non-significant effect of reward at the behavioral level, we suggest that in our study the quadrant associated with high-reward, that remained the same throughout the whole experiment for each participant, was suppressed in order to maximize the participants' gains (see also Preciado *et al.*, 2017). To our knowledge, the current study shows for the first time that attentional priorities, as indexed with the spatial bias vectors, can be reduced when targets are presented in a spatial location associated with a high reward value. Again, this may be specifically related to some specific aspect of the design, for instance including reward and goal signals that were incongruent to each other on some of the trials. Nonetheless, these findings contribute to the development of a new approach of attentional priorities/priority maps considering that attentional signals, albeit manipulated independently (see also Beffara *et al.*, 2022) are actually processed in interaction with each other via enhancement/suppression mechanisms (see also Hickey & Peelen, 2015; Won *et al.*, 2020; Adam & Serences, 2021; Zhang *et al.*, 2021 for works on distractor suppression, and Geng, 2014; Geng & Duarte, 2021 for reviews).

4.4.3 Interaction between reward and salience signals in the occipital cortex

The main aim of the current study was to manipulate at the same time goals, reward and salience, so as to assess the dependence between the processing of these signals at the occipital level. While the behavioral results suggested that reward and salience were processed independently (i.e. effect of salience, but not reward, cf. above), we found an interaction between these 2 factors when considering distributed spatial representations in the occipital cortex: salient targets increased the spatial bias towards the target quadrant, while salient distractors decreased the spatial bias. However, this was true only when targets were presented at LRL. When targets were presented at HRL, there was no significant effect of salience/display-condition. The interplay between reward and salience support previous claims of some commonalities between these two types of signals. In a behavioral study, Qin and colleagues (2021) showed that stimuli at a location previously cued with a high-reward item were perceived as more salient than stimuli cued

with a middle- or no-reward item, consistent with the hypothesis that reward-associated stimuli are processed as “more salient” stimuli (Hickey & Peelen, 2015; Qin *et al.*, 2021). Conversely, in our experiment, the suppression of the HRL may have also decreased the perceived salience of the salient target (STD_{HRL} condition), in turn making salient and non-salient targets at HRL more similar to each other (STD_{HRL} vs. HD_{HRL}).

However, these results do not explain why we found an interaction between reward and salience at the occipital level, but not at the behavioral level. This discrepancy was not predicted: we expected that in case of an interaction between reward and salience, we would obtain consistent results both at the brain and at the behavioral level. A possible explanation is that processing steps beyond the occipital cortex further modulated the effects of reward (and its interaction with salience), so that any initial processing bias (i.e. in the occipital cortex) would then be suppressed at a later stage yielding to the final behavioral output that we observed. Accordingly, we sought to investigate the effects of reward (and salience) beyond the occipital visual areas using whole-brain analyses.

4.4.4 Whole-brain mechanisms of reward and salience processing

Attention is known to be controlled by a network encompassing brain regions of the dorsal parietal and frontal cortices (cf. Corbetta & Shulman, 2002; Vossel, Geng, *et al.*, 2014 for reviews). For reward signals, a contribution of regions of the reward system (e.g. see Anderson, Laurent, *et al.*, 2014; Anderson, 2016; Anderson, Kuwabara, *et al.*, 2017) has also been evidenced, which suggests that both systems interact for the control of attention when reward signals are at play (Bourgeois, Sterpenich, *et al.*, 2022). Here, we found no significant modulation of these 2 systems in HRL compared to LRL. However, we found higher activity in the caudate nucleus for the delivery of high than low rewards (+100 rewards > +1 rewards).

This increased activity in the reward system when high reward vs. low reward was delivered confirms that our manipulation of reward efficiently drove reward-related processing. Secondly, we suggest that the specific activation in the caudate nucleus reflects the close anatomical connectivity with the occipital cortex, where we found an effect of reward (cf. above). In a fMRI study, Anderson and colleagues (2014) found that the presentation of visual stimuli associated with reward activated both the occipital cortex and the caudate nucleus. This pathway may be particularly active during visual tasks involving reward. The display they used (cf. Introduction) was similar to the one we used here, which may explain why we found similar brain activation. We plan to carry out additional analyses of inter-regional connectivity with the current dataset to specifically address this hypothesis concerning the interaction between the reward system and spatial representations in the occipital cortex (cf. also Beffara *et al.*, 2022).

While the activation of the caudate during the delivery of high-reward shows that our points-manipulation was able to drive responses in the reward system, it does not explain why HRL vs. LRL conditions did not differentially recruit neither the attention control network nor and the reward system, during the stimulus-display phase of the trail. As mentioned above, our behavioral and spatial bias occipital analyses suggest that the HRL was actually suppressed to avoid any behavioral performance impediment due to the task-irrelevance of this reward signal (see also Buschsulte *et al.*, 2014; Preciado *et al.*, 2017). Because here the suppression should have applied at the level of the spatial representation of the HRL, which was invariant, this may have depended on anticipatory proactive mechanisms. Such mechanisms have been shown to involve a disengagement of the frontoparietal attention control system (Won *et al.*, 2020; Geng & Duarte, 2021; Zhang *et al.*, 2021), suggesting that it could be directly observed in the occipital cortex without any further recruitment of high control systems. Here, from the results obtained at the whole-brain level, we suggest that similar mechanisms were at play in order to proactively suppress the HRL.

Salience, however, triggered changes in the dorsal frontal cortex. This is congruent with previous studies that investigated the effect of exogenous attention on whole-brain responses (e.g. Buschman & Miller, 2007; Melloni *et al.*, 2012; Ibos *et al.*, 2013; Bowling *et al.*, 2020, and see Corbetta & Shulman, 2002; Thompson & Bichot, 2005; Vossel, Geng, *et al.*, 2014 for reviews). Particularly, the SDD condition elicited higher responses in the left middle frontal gyrus than the STD condition. These results fit previous findings that showed increased activity in regions of dorsal frontoparietal attentional network (Won *et al.*, 2020; Zhang *et al.*, 2021), and suggest that the processing of signals (here salience) that do affect search abilities relies on the functioning of this network. Importantly, and as mentioned in the discussion of the interaction between reward and salience at the occipital level, this whole-brain effect of salience can reflect mechanisms – not directly relying in computations at the occipital level – accounting for the effect of salience at the behavioral level in the HRL-condition. Thus, based on the current results we suggest that interactions between occipital cortex and higher-level system may, on the one hand, mediate the effect of salience on behavior in the HRL condition and, on the other hand, suppress the overall effect of reward that - in the current study - did not result in any modulation of behavioral performance.

4.5 CONCLUSION

We assessed how goals, salience and reward interact in the occipital cortex. We used spatial bias vectors to quantify to what extent the spatially distributed patterns of activity in the occipital cortex were biased towards the representation of the target location. We found that reward did not affect behavioral performance, but nonetheless we observed a

decreased spatial bias towards the target location when that location was associated with high vs. low reward. Further, the effect of salience at the occipital level was observed only when the target was presented at a location associated with low reward. Together, these results suggest that reward interacts with goals and salience for processing in the occipital cortex, but also that this is not directly reflected in the final behavioral output. We suggest that the additional involvement of the dorsal fronto-parietal attentional network may explain this apparent discrepancy. In any case, the current results show that reward-signals can, in specific task conditions, lead to representation suppression rather than enhancement, as dominantly accepted. Together, these findings specify new constraints governing the attribution of attentional priorities in the occipital cortex and indicate new directions to better understand the effect of reward on spatial attention.

Chapter 5

General discussion

As currently formalized, the priority maps framework (see Awh *et al.*, 2012; Ptak, 2012; Macaluso & Doricchi, 2013; Todd & Manaligod, 2018; Bisley & Mirpour, 2019) posits that attentional signals (e.g. goals, physical salience, statistical regularities, reward, emotions, social information, etc) located across the visual field are represented in so-called “priority maps” in spatially-selective brain areas (e.g. occipital cortex, dorsal parietal and frontal cortices). These signals’ representations compete in order to determine what region of the visual field should be selected and attended. Recent imaging studies confirmed that different types of attentional signals are represented in the occipital visual cortex (see Kastner, Pinsk, *et al.*, 1999; Melloni *et al.*, 2012; Buschsulte *et al.*, 2014; Sprague *et al.*, 2018; Won *et al.*, 2020; Adam & Serences, 2021; Grahek *et al.*, 2021; Zhang *et al.*, 2021), but also raised new questions: What happens when different types of attentional signals are present at the same time in the visual field? Do attentional priorities affect activity at the different levels of the visual processing hierarchy in the same way? What mechanisms govern the setting of these priorities? To address these issues, I designed three fMRI experiments that aimed to better understand how current goals (all experiments), statistical regularities (Experiment 2), reward (Experiment 3) and physical salience (all experiments) jointly affect the distributed patterns of activity across different levels of the visual hierarchy in the occipital cortex.

In the first experiment, I tested the interplay between goals and physical salience. I showed that both signals affected spatial representations at the three levels of the visual hierarchy that were considered here (BA17, BA18 and BA19). In each BA, the activity was biased towards the representation of the spatial location where the target was presented (goal-related signal). The spatial bias increased when the visual display included a salient target and was reduced when the display included a salient distractor (salience-related signal). However, the results of the behavioral analyses showed marginal effects of salience, suggesting that additional mechanisms counteracted the impact of salience on the final behavioral output (see also Sprague *et al.*, 2018, and Geng, 2014; Geng & Duarte, 2021 for reviews). Analyses of effective connectivity between

the PPC and the occipital cortex showed that displays comprising a salient distractor elicited a top-down enhancement from the PPC to the occipital region representing the target, which I interpreted as evidence of a mechanism counteracting the effect of the salient distractor (see also Chelazzi, Marini, *et al.*, 2019, for a recent review of suppression/enhancement processes).

The second experiment explored the contribution of goals, physical salience and statistical regularities in the guidance of attention. The results revealed that all the three BAs represented current goals and salience (as in Experiment 1), again with a systematic spatial bias towards the visual representation of the target quadrant. However, there was now an exception to this: activity in BA17 was biased toward the target location only when the target was presented at the low target probability location. This result supports the notion that statistical regularities about the target location/presence lead to "sensory expectation suppression" in early visual areas (see Richter & de Lange, 2019; Alink & Blank, 2021). By contrast, statistical regularities did not affect spatial biases in areas BA18 and BA19. The finding that statistical regularities modulated responses only in BA17 suggests that the underlying mechanism is not due to feedback signaling from higher visual areas, otherwise statistical regularities would have been found to affect also BA18 and BA19 (cf. Adam & Serences, 2021). The latter was confirmed further by analyses of interregional connectivity that showed changes in functional coupling between the PPC and BA18/19 – but not BA17 – as a function of the target probability location. This is consistent with the hypothesis that bottom-up mechanisms, rather than top-down signaling, mediate sensory expectation suppression in BA17. At variance with Experiment 1, the behavioral analyses now revealed that both statistical regularities and salience affected performance, with the fastest reaction times recorded for salient targets presented at the high-probability location. Nonetheless, the two factors did not significantly interact, suggesting that - in this experiment – there was no competitive interactions between the two signal-types.

In the third experiment, I manipulated goals, physical salience (cf. Experiments 1-2) and the rewarded location. I found that salience, but not reward, modulated behavioral performances. At the brain level, the spatial bias towards the target quadrant was weaker when the target was presented at the highly rewarded location compared to when it was presented at a poorly rewarded location. I interpreted both behavioral and brain findings as evidence of suppression of the reward-signal, because - in my study -reward was irrelevant for accurate task performance. Indeed, to be rewarded at the end of the experiment, participants had to correctly discriminate the target as fast as possible on a maximum of trials. Specifically focusing attention on the highly rewarded location would impede correct and fast target discrimination at other locations, thus minimizing the overall task performances (see also Buschschulte *et al.*, 2014; Hickey & Peelen, 2015;

Preciado *et al.*, 2017 for studies showing/discussing task impediment by reward signals). Moreover, the imaging results revealed an interaction between salience and reward in all three BAs in the occipital cortex, with target salience increasing the spatial bias towards the target quadrant and distractor salience decreasing it (see also Experiment 1), but only when the target was presented at a low-reward location.

BA/Behavior	Goals	Salience	Statistical regularities	Reward	Salience x statistical regularities	Salience x reward
EXPERIMENT 1						
BA17	✓	✓				
BA18	✓	✓				
BA19	✓	✓				
BEHAVIOR		~				
EXPERIMENT 2						
BA17	x	✓	✓*		x	
BA18	✓	✓	x		x	
BA19	✓	✓	x		x	
BEHAVIOR		✓	✓		x	
EXPERIMENT 3						
BA17	✓	✓		✓*		✓
BA18	✓	✓		✓*		✓
BA19	✓	✓		✓*		✓
BEHAVIOR		✓		x*		x

Figure 5.1: **Summary table of the main effects and interactions in all BAs, plus at the behavioral level, across the three experiments.**

Check and cross signs accompanied with a star are effects that do not fit the initial priority maps proposal.

As mentioned above and in the Introduction, most of my predictions derived from the priority maps framework. In all three experiments, I obtained results in line with my initial predictions, and consequently supporting this framework. For example, I found spatial signatures of goal-related and salience-related signals, comprising an increase of brain activity in occipital regions that represent the corresponding spatial locations (see also Sprague *et al.*, 2018). However, in all the three experiments, I also found results that could not be directly predicted in priority maps framework (cf. figure 5.1). For example, in Experiment 1 salience had a weak effect at the behavioral level, while it was reliably represented in the occipital cortex. In Experiment 2, targets presented in the expected quadrant induced a reduction – rather than an enhancement – of the spatial bias towards the target representation in BA17 (see Theeuwes, 2018; Richter & de Lange, 2019; Alink & Blank, 2021). In Experiment 3, targets presented in the highly rewarded quadrant were not easier to discriminate than targets presented in the poorly rewarded quadrant (at variance with results in Anderson, Laurent, *et al.*, 2011; Chelazzi, Estocinova, *et al.*, 2014). Furthermore, targets at the high-reward location were associated with a reduction - rather than an enhancement – of the spatial bias towards the target quadrant. In the following sections, I will discuss these apparent inconsistencies with the aim of integrating these unexpected findings in the priority maps framework.

5.1 Combining brain and behavioral approaches to evidence enhancement and suppression mechanisms

Attentional priority can be observed at the behavioral level, for example when performance is higher in a salient target condition than in a homogeneous display condition (cf. behavioral results in Experiments 2-3). Importantly, the mechanisms linking brain responses and the final behavior are complex, so that neural signatures of priorities may not intuitively reflect behavioral priorities.

The priority maps framework has mostly been formalized in review articles (Awh *et al.*, 2012; Ptak, 2012; Todd & Manaligod, 2018; Bisley & Mirpour, 2019; Anderson, 2021). Although the theoretical framework has been applied to explain results at different levels (e.g. behavior, neural networks at the mesoscopic scale, single-cell electrophysiology, etc), most of the supporting experimental evidence considered only one level at the time (see Chelazzi, Estocinova, *et al.*, 2014; Ferrante *et al.*, 2018 for behavioral studies and Sprague *et al.*, 2018 for a fMRI/mesoscopic investigation). While these studies are of primary interest for the understanding of how attentional priorities are computed, they cannot fully capture the integrated effects of attentional signals. This encourages the stereotyped view according to which enhanced behavioral performance is caused by increased brain responses within the priority maps (Bisley & Mirpour, 2019). Recently, the relationship between brain and behavior, that better fits the priority maps theoretical framework, has gained interest (Melloni *et al.*, 2012; Won *et al.*, 2020; Adam & Serences, 2021; Zhang *et al.*, 2021, and the three experimental chapters of this thesis). For example, this permitted highlighting how suppression and enhancement at the brain level jointly account for the attribution of attentional priorities at the behavioral level (Geng & DiQuattro, 2010; Geng, 2014; Anderson, 2021; Geng & Duarte, 2021; Luck, Gaspelin, *et al.*, 2021). Below, I detail how the three experiments of my thesis contribute to specify the complex mechanisms that link brain and behavior during the attribution of attentional priorities, in particular via enhancement and suppression mechanisms.

As a brief reminder, in Experiment 1 I used 100% predictive cues that indicated on each trial the quadrant where the target would appear, before the presentation of the stimulus-display. There were three possible display-conditions: the display could either contain four bars of the same color, or a salient target, or a salient distractor. The display-conditions operationalized the effect of salience. While I found only a residual effect of salience at the behavioral level, the imaging data revealed reliable signatures of both goals and salience in the occipital cortex: the spatial bias towards the representation of the target quadrant increased for salient targets and decreased in the presence of salient distractors (see Sprague *et al.*, 2018 for related results). In the priority maps framework,

given these imaging results, it would be expected that salient targets would also be associated with a behavioral advantage, and salient distractors with a behavioral performance impediment (e.g. see Melloni *et al.*, 2012; Won *et al.*, 2020), which was not the case here. These apparently surprising results points to the interest of considering the relationship between the brain and the behavioral approaches. In the context of Experiment 1, I put forward that the (lack of) salience-related modulation of the behavioral responses was due to the high level of engagement of endogenous attention (100% predictive cues) towards the target quadrant. The latter would suppress the effect of stimulus-driven salience. In a related EEG study, also conducted as part of the MAC-Brain project, Rashal and colleagues (2022) showed that indeed the effect of salience on behavioral performance was attenuated when using 100% predictive cues compared with a no cue condition. Together, these findings provide us with new evidence about the relative weight of the different signals (here goals and salience) in the attribution of attentional priorities.

However, recent studies focusing on the brain mechanisms underlying the reduction of the effect of salient distractors on behavioral performance highlighted that the representation of the salient distractor in the occipital cortex is also reduced (Won *et al.*, 2020; Adam & Serences, 2021; Zhang *et al.*, 2021). Basically, at the brain level, the occipital cortex does not differentiate any more between salient and non-salient distractors (Won *et al.*, 2020). This mechanism of salience suppression would explain my behavioral results, but it is not compatible with my brain data showing instead that salience still modulated activity in the occipital cortex. Another possible explanation of the different effects of salience on brain versus behavior concerns the processing of stimuli in the target quadrant. In particular, the analyses of effective connectivity revealed a top-down enhancement of the influence of PPC on the target’s occipital representation, rather than a suppression on the salient distractor’s representation. This would fit the idea of a “reactive enhancement” mechanism, boosting target processing when the display also contained a salient distractor, which presence could not be anticipated (see Geng, 2014; Chelazzi, Marini, *et al.*, 2019; Geng & Duarte, 2021). Moreover, Rashal and colleagues (2022) showed that the N2pc (an event-related potential associated with target selection) was absent in trials including a 100% predictive cue, while it was present in no-cue trials (see also Luck, 1995). This suggests that fully-predictive cues make the task very easy, with attention being already fully focused on the target quadrant before the presentation of the visual display. This phenomenon can be considered a mechanism of “proactive enhancement” (as compared with the notion of “proactive suppression”, see Geng, 2014; Geng & Duarte, 2021 and see Chelazzi, Marini, *et al.*, 2019 for a review on enhancement/suppression mechanisms), that would increase the focus towards the target location rather than suppressing the salient signals. This would explain why I observed an effect of salience at the brain level, without any corresponding modulation on the final behavioral responses.

In order to further argue in favor of this claim, I re-computed the effect sizes associated with the goal-related effects in the occipital cortex (ROI_IN versus ROI_OPP) for each of the three experiments, but only for the conditions that did not entail any suppression: that is, for Experiment 1, I computed the effect size irrespective of the salience and BA; for Experiment 2, I excluded responses in BA17 for the high target-probability location condition (see Chapter 3, and next paragraphs); for Experiment 3, I excluded data corresponding to the presentation of the target in the highly rewarded quadrant (see Chapter 4, and next paragraphs). I first performed a paired T-test to compare ROI_IN and ROI_OPP responses, which yielded a significant effect ($p < 0.001$) in all three experiments. This reflects the increased activation of the representation of the target quadrant compared to the distractor representation (effect of the “current goal”) that was consistently observed in the three experiments. The effect sizes (Cohen’s d) of this comparison were 2.48, 1.27 and 1.12 respectively for Experiment 1, Experiment 2 and Experiment 3 (see figure 5.2A). The main difference between Experiment 1 and Experiments 2-3 is that Experiment 1 included fully predictive cues, while no cues were used in Experiments 2-3. In addition, in Experiment 1 the tilted target was easier to discriminate from the distractors that were either vertical or horizontal than in Experiments 2 and 3, where all stimuli were tilted. Here, I cannot tease apart the contribution of cue-presence versus target discrimination difficulty, but the difference in effect sizes suggests that the attentional focus towards the target quadrant was larger in Experiment 1 than in Experiments 2-3. On that basis, I propose that the larger the bias towards the target location (difference between ROI_IN versus ROI_OPP), the less stimulus-driven salience affects behavioral performance, which supports the proactive enhancement interpretation. In sum, Experiment 1 showed that salience-related modulation of activity in the occipital cortex is not necessarily associated with analogous effects at the behavioral level. This highlights the importance of considering attention priorities both at the behavioral and brain levels, and suggests the existence of multiple co-occurring mechanisms that should be accounted for in the priority maps framework (see e.g. Awh *et al.*, 2012, and see Luck, Gaspelin, *et al.*, 2021 for an update of the framework now including enhancement/suppression components).

In Experiment 2, I observed a loss of the spatial specificity of the spatial bias in BA17, when the target was presented at the high target-probability location. Beyond the fact that it occurred only in BA17 (this will be discussed in a following section), the priority maps framework would predict the reverse pattern, i.e. increased spatial bias towards the target quadrant when the target was presented at the high target-probability location (cf. also Ferrante *et al.*, 2018). Nonetheless, it should be noticed that weaker responses for expected features/locations are now also well documented (Richter & de Lange, 2019; Won *et al.*, 2020; Adam & Serences, 2021; Alink & Blank, 2021; Zhang

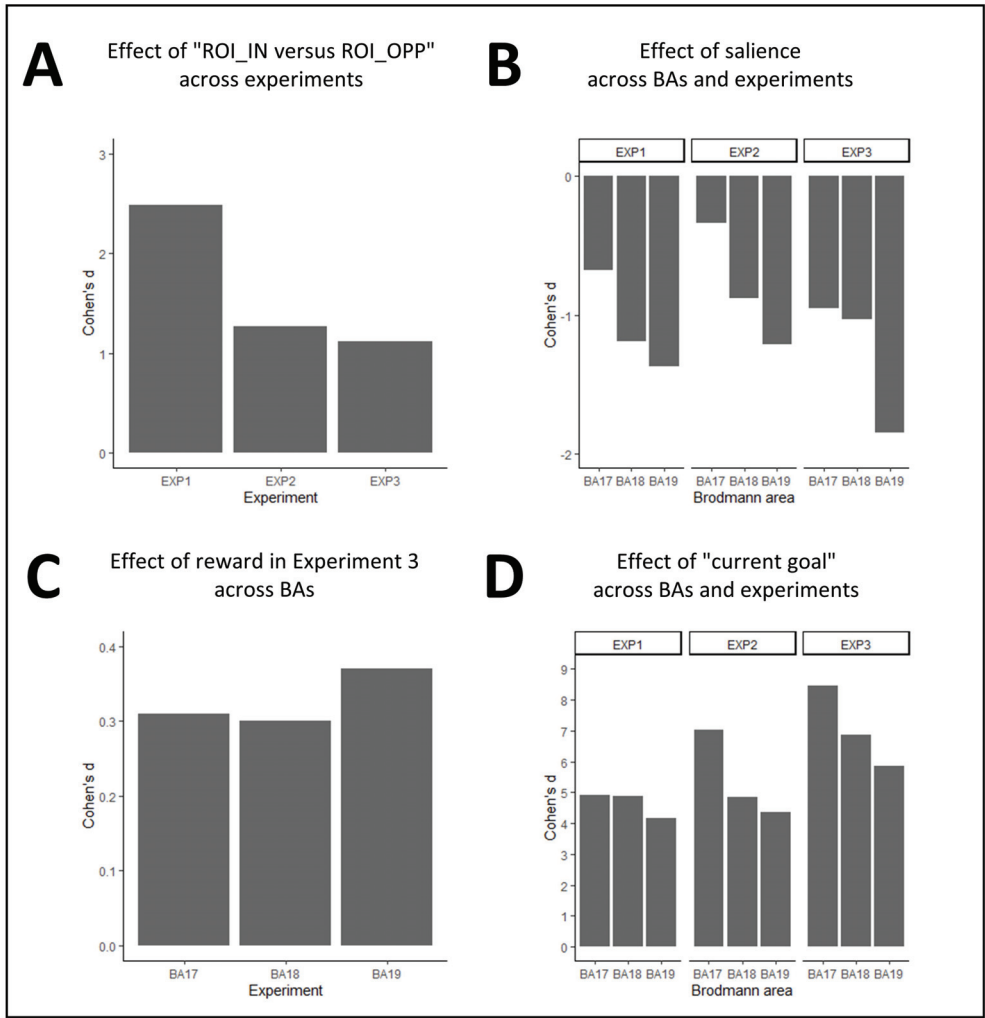


Figure 5.2: **Magnitude of the effects of goals, salience and reward.**

A - Descriptive effect size of the “ROI_IN versus ROI_OPP” comparison across experiments. **B** - Descriptive effect size of the “STD minus SDD” spatial bias across BAs and experiments. All effect sizes are negative because spatial bias vectors in STD are closer [smaller distance from the target quadrant representation] to the target quadrant representation than in SDD [higher distance from the target quadrant representation]. The more negative the effect size, the more important the effect of salience. **C** - Descriptive effect size of the “HRL minus LRL” spatial bias across BAs and experiments. Effect sizes are positive because the spatial bias vectors in HRL are further away from the target quadrant representation than in LRL, cf. Chapter 4). **D** - Descriptive effect size of the spatial bias distance from the target quadrant representation across BAs and experiments. Smaller effect sizes signify higher spatial bias towards the target quadrant representation [lower distance from the target quadrant representation].

et al., 2021). The latter is thought to occur as a consequence of distractor suppression mechanisms (Won *et al.*, 2020; Adam & Serences, 2021; Zhang *et al.*, 2021), but also because of “sensory expectation suppression”. The latter would comprise local processing mechanisms specifically related with the repeated presentation of a specific item (e.g. a salient stimulus, Won *et al.*, 2020; Adam & Serences, 2021; Zhang *et al.*, 2021). The investigation of statistical regularities associated with distractor stimuli largely

contributed to the understanding of suppression mechanisms (Won *et al.*, 2020; Adam & Serences, 2021; Zhang *et al.*, 2021). However, these studies do not allow us to dissociate proactive distractor suppression from sensory expectation suppression (see also Chapter 3). In Experiment 2, I was able to dissociate sensory expectation suppression from proactive distractor suppression: the behavioral results showed that the processing of targets presented at the high probability location was facilitated, but the pattern of occipital activity in BA17 showed suppression, which could only be ascribed to sensory expectation suppression, otherwise behavioral performances would have been similar between targets presented at HTPL versus LTPL (reflecting suppression at HTPL, see Won *et al.*, 2020). In the priority maps framework, these results raise the question of whether expectation suppression affects other spatial maps in the brain and, most important, what specific mechanisms mediate expectation suppression (e.g. top-down versus bottom-up processing, see also sections below). To my knowledge, this has never been addressed even in the most recent updates of the priority maps framework (Anderson, 2021; Luck, Gaspelin, *et al.*, 2021).

In Experiment 3, I found a reduction of the spatial bias towards the target quadrant when targets were presented in the highly rewarded quadrant. Stimuli associated with high reward are known to capture attention more than neutral stimuli or stimuli associated with low reward (Pessoa, 2010; Anderson, Laurent, *et al.*, 2011; Awh *et al.*, 2012; Chelazzi, Perlato, *et al.*, 2013; Chelazzi, Estocinova, *et al.*, 2014; Anderson, 2016; Anderson, Kuwabara, *et al.*, 2017). Thus, at the brain level my results appear to challenge these straightforward predictions of the priority maps framework (see also Chelazzi, Estocinova, *et al.*, 2014, who anticipated an increased gain in the spatial priority map corresponding to the highly rewarded location). In Experiment 3, I suggest that the task configuration made reward irrelevant – or even counterproductive – to maximize the attentional bias towards the highly rewarded quadrant (Chelazzi, Estocinova, *et al.*, 2014). This is because the task required the participants to be both fast and accurate on each trial in order to maximize their chances to get a reward at the end of the experiment: excessive attentional prioritization of the highly rewarded quadrant would rather minimize the participants' chances to correctly/fastly detect targets in the other quadrants.

In sum, I discussed some of the results obtained in the three studies of my thesis and highlighted the interest of considering together the brain responses in the occipital cortex and the behavioral outcome of the manipulations of goal, salience, statistical regularities and reward. Taken separately, brain and behavior provide us only with a partial view of the mechanisms that govern the allocation of attentional priorities and can lead to wrong or incomplete predictions about these mechanisms. The methodology employed in my three experiments permitted addressing this and to obtain a more balanced view of how

multiple priority signals jointly contribute to setting attentional priorities. In particular, altogether, the three studies shed new light on the mechanisms underlying enhancement and suppression phenomena that had remained elusive so far (see Geng, 2014; Chelazzi, Marini, *et al.*, 2019; Geng & Duarte, 2021 for reviews). Further, beyond the combination of brain and behavior measures, I suggest that the use of effective (Experiment 1) and functional (Experiment 2) connectivity analyses constitute powerful tools to investigate these mechanisms in more details (see next section).

5.2 Feedforward and feedback mechanisms

The three experiments comprised the study of occipital responses at three levels of the visual hierarchy (BA17, BA18 and BA19), and of changes of activity at the whole-brain level. Experiments 1-2 also included analyses of interregional connectivity. These analyses targeted the interplay between regions involved in attention control (i.e. regions of the dorsal frontoparietal attentional, see Corbetta, Kincade, *et al.*, 2000; Corbetta & Shulman, 2002; Vossel, Weidner, *et al.*, 2012; Vossel, Geng, *et al.*, 2014) and the occipital cortex where I found modulations related to the different attentional signals, see sections above. Traditionally, the effect of goals in the occipital cortex is thought to arise from top-down/feedback signals originating in frontoparietal areas (see e.g. Kastner, Pinsk, *et al.*, 1999; Martínez *et al.*, 1999; Yantis, 2005; Vossel, Weidner, *et al.*, 2012), while the effect of salience observed in occipital areas is generally associated with exogenous/bottom-up/feedforward control (see Beck & Kastner, 2005; Yantis, 2005). The mechanisms governing statistical regularities and reward processing are, to date, still debated (Theeuwes, 2018). My current results provide us with several new elements to better understand the contribution of top-down/bottom-up signaling to these mechanisms.

5.2.1 Salience-related mechanisms

I will first focus on physical salience that was manipulated in all my three experiments. The assumption that salience relies on bottom-up processing implies that salience is represented in early visual areas (see e.g. Chen *et al.*, 2016) and competes with goal-related signals in higher visual areas (see Corbetta & Shulman, 2002, and figure 1.5). However, the data of my experiments - as well as theoretical and experimental works (Itti & Koch, 2001; Yoshida *et al.*, 2012; Betz *et al.*, 2013; Veale *et al.*, 2017) - seem to tell a different story. Indeed, while it is true that salience affects responses in V1/BA17 (Melloni *et al.*, 2012; Betz *et al.*, 2013; Sprague *et al.*, 2018 and the three experiments here), this does not signify that salience is computed in this area: salience may be computed at some other level of the visual hierarchy that would then affect activity in BA17/V1. Here, a key issue concerns what specific features are coded in the different levels of the visual hierarchy. The pioneer neurophysiology work that investigated the role of V1/BA17 in vision (Hubel & Wiesel, 1959) found that V1 neurons predominantly coded stimulus

orientation. Related to salience processing, Yoshida and colleagues (2012) had monkeys to watch visual scenes including more or less salient items, before and after a V1 ablation. In ablated monkeys, all visual features (motion, color, etc) equally contributed to the gaze guidance towards the most salient stimuli compared to non-ablated monkeys, with the exception of orientation. This means that stimuli that were salient on the basis of their singular orientation were no more processed as salient items. This shows that V1/BA17 contributes to the processing of salience specifically related to stimulus orientation (but see Chen *et al.*, 2016) and it is compatible with a mechanism where features are first analyzed independently to compute feature-dependent maps (e.g. orientation map in V1 hypothetically) that are then summed into feature-independent saliency maps (Itti & Koch, 2001; Veale *et al.*, 2017). In this view, the earliest level that could contain saliency maps would be BA19, because at this stage most – if not all – features contributing to salience have been analyzed (e.g. BA17 for orientation, BA18 for shapes, etc; see figure 1.3). This corresponds to a bottom-up/feedforward mechanism of salience computation, as suggested in Corbetta & Schulman (2002). However, considering this view, the salience signatures observed in BA17 (Melloni *et al.*, 2012, and my three experiments) are necessarily due to some feedback signaling from saliency maps located in higher level visual areas.

In all my experiments, salience was found to modulate activity in all three BA regions. Importantly, these effects cannot be due to feature-specific processes in BA17 and BA18, because I used color singletons to operationalize salience – which cannot be detected in BA17/18 – and I equated the luminance of all stimuli. Following the hypothesis according to which the effect of salience in BA17 and BA18 is due to feedback signaling, I explored whether the magnitude of this effect changed along the visual hierarchy. In particular, if salience is computed in BA19, its magnitude may be larger than in BA18 and BA17. I should stress that this is a very indirect way of testing the feedback hypothesis, but this rationale has been used to account for an indirect effect of distractor suppression in higher visual areas in a previous work (Adam & Serences, 2021). Accordingly, I computed the effect size (Cohen’s *d*) of the impact of salience on the spatial bias (i.e. the distance from a virtual spatial bias towards the target quadrant representation, see the Method sections of Chapters 3 and 4) separately for all BAs and all experiments. Specifically, I considered the difference between “salient target” minus “salient distractor” conditions. For Experiment 3, I excluded the data corresponding to targets presented in the highly rewarded quadrant, because in this condition there was no significant effect of salience (see Chapter 4). I predicted a decreasing effect size from BA19 to BA17, accounting for an increasingly indirect effect of salience at the different levels of the visual hierarchy. For Experiment 1, I obtained a Cohen’s *d* of -1.37 in BA19, -1.19 in BA18 and -0.68 in BA17. For Experiment 2, the effect sizes were of -1.21, -0.88 and -0.34 respectively for BA19, BA18 and BA17. They were of -1.85, -1.03 and -0.95 in Experiment 3 for

BA19, BA18 and BA17 respectively (see figure 5.2B). Note that all the effect sizes here are negative because the distance from the “virtual” target position was further away [larger distance] for the salient distractor condition, i.e. a weaker spatial bias towards the target representation, than for the salient target condition [smaller distance]. These descriptive results corroborate the view according to which the spreading of the salient signals take place in a feedback manner, from higher to lower visual areas. Note, however, that the saliency map may be computed in even higher-order areas, for example in regions of the dorsal frontoparietal attention control network (Buschman & Miller, 2007; Gottlieb, 2007; Ptak, 2012; Veale *et al.*, 2017). In this case, I would expect larger effect sizes in dorsal regions of the frontoparietal network than in BA19 (but see next paragraph).

My second argument in support of feedback mechanisms of salience processing is based on the effective connectivity analyses of Experiment 1. These assessed changes of the directional influences between the PPC and the spatially-specific BA18 ROIs, as well as between BA18 ROIs, as a function of the display-condition. The results showed that the salient distractor condition, compared with homogeneous display, lead to an increased feedback connectivity from the PPC to the BA18 “ROI_IN” (spatial representation of the target quadrant), along with changes of connectivity between the four BA18 ROIs. This reactive target enhancement mechanism (cf. above) further supports the view according to which salience can be processed also via top-down/feedback signaling, at least in tasks comprising a strong weight of goal-directed signals (cf. Chapter 2).

My third argument concerns the results of Experiments 2 and 3. At variance with Experiment 1, I now found that salience did influence the behavioral responses (i.e. salient targets increased performance, while salient distractors decreased performance). The whole-brain analyses showed that in both studies the presence of salient distractors was associated with activation of the dorsal fronto-parietal attention control network. In figure 5.3 below, I overlaid the contrast images for the SDD > STD contrast (salient distractor display > salient target display) of Experiment 2 and Experiment 3, highlighting the common whole-brain correlates of salience processing in the two studies. This included common activation of the left superior frontal sulcus, most likely including the frontal eye-fields. These results do not directly support the role of top-down signaling, but demonstrate that salience computations involve also areas outside the occipital cortex (cf. also Won *et al.*, 2020; Zhang *et al.*, 2021 who reported significant activation increases in areas of the frontoparietal network in the presence of salient distractors compared to no salient distractor present). In sum, the processing of salience may require computations both at the occipital and at the fronto-parietal levels, which may be causally linked under specific task constraints (see previous paragraph, and Experiment 1 effective connectivity results).

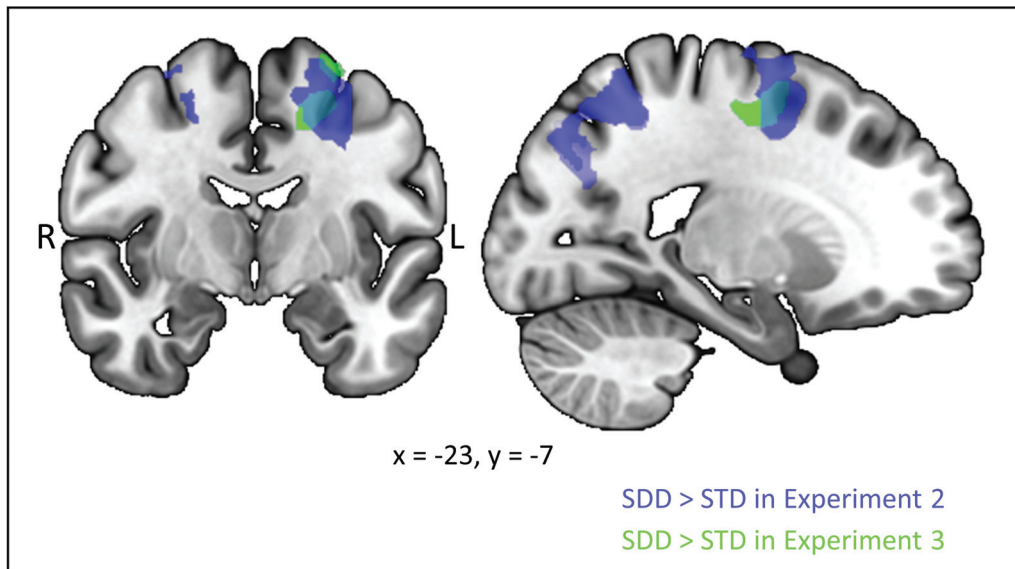


Figure 5.3: Map of significant activation at the whole-brain level for the SDD > STD contrast, in Experiments 2 (blue) and 3 (green).

This shows an overlap in the left superior frontal sulcus for the SDD condition that comprised the salient distractors. Threshold: p-FWE-corrected = 0.05 at the cluster level, with cluster-size defined at a voxel-wise threshold of p-uncorrected = 0.005.

5.2.2 Reward- and statistical regularities-related mechanisms

Beside the effect of salience, my results contribute to the top-down/bottom-up debate by examining signals that have been often neglected in traditional accounts of attention control (see Corbetta & Shulman, 2002; Chica, Bartolomeo & Valero-Cabre, 2011; Chica, Bartolomeo & Lupiáñez, 2013; Vossel, Geng, *et al.*, 2014), i.e. statistical regularities and reward (see Awh *et al.*, 2012; Theeuwes, 2018; Todd & Manaligod, 2018 for reviews). The role top-down/bottom-up signaling has emerged from the proposal that statistical regularities, and reward biases, should not be considered merely as additional sources of top-down control (as in e.g. Wolfe *et al.*, 2003; Melloni *et al.*, 2012), but rather as new category of attentional signals (see Awh *et al.*, 2012; Theeuwes, 2018 for reviews). Although reward and statistical regularities have been both categorized as “selection/trial history” signals, it is accepted that they are not supported by the same brain mechanisms. For example, Anderson and colleagues (2017) showed that, in an attentional task, the magnitude of the dopamine release in the caudate nucleus evoked by a distractor stimulus associated with high reward was positively correlated with the magnitude of the corresponding behavioral impediment. Thus, reward-signaling relies on the activation of the reward system (see e.g. Anderson, 2016; Anderson, Kuwabara, *et al.*, 2017). By contrast, studies that manipulated statistical regularities pointed to a key role of regions of the dorsal frontoparietal system (e.g. Won *et al.*, 2020; Zhang *et al.*, 2021). Nonetheless, both types of priority signals have been also associated with activation of the dorsal fronto-parietal network (Won *et al.*, 2020; Zhang *et al.*, 2021, Bourgeois, Sterpenich, *et al.*, 2022 for reward). These common brain correlates involving the

fronto-parietal attention control network suggest that reward and statistical regularities do not take place in a fully bottom-up manner. However, Theeuwes (2018) reviewed evidence showing important similarities between bottom-up, stimulus-driven salience and reward/statistical regularities processing: both types of signal bias attentional control rapidly, these biases are “automatic” and take place effortlessly. In fact, these observations support the notion that reward- or regularities-associated stimuli become “more salient”, because of some change in their perceptual representations (Theeuwes, 2018, see also Todd & Manaligod, 2018). Studies focusing on the brain mechanisms governing the processing of statistical regularities have mainly focused on the regularities/learning of distractor’s features/location, which may be confounded with distractor suppression mechanisms involving top-down control (Won *et al.*, 2020; Adam & Serences, 2021; Zhang *et al.*, 2021). So, they could not completely rule out the possibility that statistical regularities were encoded automatically in the occipital cortex in a bottom-up manner (see Adam & Serences, 2021; Alink & Blank, 2021).

Experiment 2 allowed me to address these issues by examining changes associated with the manipulation of the target - rather than distractor – probability location. The latter should minimize any contribution of active, top-down distractor suppression. In BA17, the results showed that targets presented at the high probability location were associated with a weaker spatial bias than targets presented at the low probability location, consistent with an expectation suppression phenomenon in the very early stages of visual processing (Richter & de Lange, 2019; Alink & Blank, 2021). In addition, the analyses of functional connectivity did not reveal any significant effect of high/low probability on the functional connectivity between BA17 and the PPC in the dorsal fronto-parietal network. This suggests that target location expectations are mapped early in the visual hierarchy, in a bottom-up fashion. By contrast, the connectivity analyses revealed a significant increase of the functional coupling between PPC and BA18/19, when targets were presented at the low-probability location. Although these analyses do not allow me to interpret the results as evidence of a directional, top-down effect from the PPC to BA18/19, they support the notion that statistical regularities engage also higher-level mechanisms involving interactions between the dorsal fronto-parietal control network and the occipital cortex. Accordingly, based on Experiment 2, I suggest that statistical regularities are processed locally within early visual areas, but also that mechanisms involving remote influences arising from the dorsal fronto-parietal network are recruited, in particular when goal-related signals (target location) and expectation-related signals (target probability location) signals are spatially incongruent. I relate the processing in early visual cortex with sensory expectation suppression, and the engagement of (top-down) connectivity with situations requiring additional executive control to counteract a mismatch between current goals and expectations.

In Experiment 3, related issues were now addressed from the perspective of the processing of reward signals. The imaging analyses showed that targets presented at the high reward location resulted in a decrease of the spatial bias in the occipital cortex. I interpreted this as the proactive suppression of the reward signal that, in my task, could potentially lead to an impediment of goal-directed performance (cf. above). As for the case of statistical regularities (see above), the question of whether the processing of reward relies on bottom-up or top-down mechanisms is still debated (Theeuwes, 2018). For reward, however, the question may be less difficult to answer, because it seems unlikely that a reward bias can take place in the occipital cortex without any contribution from the reward system (possibly via the fronto-parietal control network, Anderson, 2016; Bourgeois, Sterpenich, *et al.*, 2022). The results of Experiment 3 showing that suppression of spatial biases in the occipital cortex were observed without any changes of activity in the frontoparietal network seems to fit the proposal that proactive suppression mediated the effect of reward in the occipital cortex. However, it should be stressed the engagement of proactive mechanisms does not forcibly imply sustained top-down feedback control. For instance, Geng & Duarte (2021) suggested that the disengagement of fronto-parietal control could reflect a modification of the strength of distraction over time (cf. also Won *et al.*, 2020): here the key point concerns the possibility that different mechanisms may govern processing in the initial phases of the task, when there is a higher incertitude about the statistical/reward contingencies versus later stages when processing priorities may be set according to the information collected over trials. This could be addressed by comparing brain responses at the beginning versus the end of the experiment, but here – as in previous studies – this was not tested directly. Such analyses could reveal whether the reward and fronto-parietal systems bias occipital regions at the beginning the experiment (proactively via top-down signaling), but disengage at the later stages when sensory expectation suppression would govern the effect of reward on attention (automatically, via local processing in the occipital cortex). Accordingly, fronto-parietal and reward systems would first “set” the proactive reward suppression in occipital regions, which would then remain on the long-term without any further contribution from these control systems.

I sought some support for this proposal using the same strategy that I applied to salience processing above (see figure 5.2). Here I suggest that if proactive suppression is a top-down mechanism originating from reward- and/or attention-specific systems, then the reward bias should be stronger in high-level visual regions (here BA19) and progressively decrease when moving down the visual hierarchy (BA18 and BA17). Accordingly, I computed the effect size of the difference between the spatial biases at the high-rewarded versus a low-rewarded quadrant. These descriptive indexes should provide me with some hint on whether the suppression observed in the occipital cortex relies on top-down versus bottom-up processes (see Adam & Serences, 2021 for a similar analysis strategy). For BA19, the Cohen’s *d* value was 0.37 (distance from the target quadrant representation when target presented in the high-rewarded quadrant > target

presented in low-rewarded quadrants). It was 0.30 in BA18 and 0.31 in BA17 (see figure 5.2C). Thus, the reduced effect of reward on the spatial bias in BA17 compared with BA19 suggests that the suppression of the reward signals in Experiment 3 was mediated via top-down signaling. Again, I concede that this is not a direct evidence of top-down signaling and these results should be seen as descriptive only. Nonetheless, in order to gain further evidence about the relevance of the analyses of effect-size across BAs, I performed a complementary control analysis. Given that there is extensive evidence that target selection/endogenous bias originates in frontoparietal areas and reaches occipital areas in a top-down manner (Kastner, Pinsk, *et al.*, 1999; Corbetta, Kincade, *et al.*, 2000; Corbetta & Shulman, 2002; Buschman & Miller, 2007; Vossel, Weidner, *et al.*, 2012; Ibos *et al.*, 2013; Vossel, Geng, *et al.*, 2014), I now computed the effect size of this well-characterized, top-down effect. For this, I considered the spatial bias vector data of Experiment 1 (all vectors-data), Experiment 2 (only in LTPL condition for BA17) Experiment 3 (only trials when target was presented in a low-reward quadrant). The HTPL data in BA17 for Experiment 2 and the high-reward data of Experiment 3 were excluded because these led to a loss of the spatial biases (see figure 4 in Chapter 3, and figure 4 in Chapter 4). For Experiment 1, I obtained a Cohen's d of 4.91, 4.87 and 4.15 respectively for BA17, BA18 and BA19. For Experiment 2, the effect sizes were 7.03, 4.85 and 4.36 respectively for BA17, BA18 and BA19. For Experiment 3, I obtained a Cohen's d of 8.47 for BA17, 6.85 for BA18 and 5.85 for BA19 (see figure 5.2D). Here, a higher effect size means an increased distance of the spatial bias vector from the target quadrant representation (i.e. a weaker effect of endogenous spatial attention). Thus, the results of this control analysis are consistent with the idea that progressive changes of the effect size across the visual hierarchy may indicate top-down versus bottom-up signaling (Adam & Serences, 2021). In turn, this brings further support to my analyses that considered the effect of high/low reward and the role of top-down influences in this (see figure 5.2C-D).

In sum, the previous two sections discussed how the data of the three experiments of this thesis contribute to better explain how attentional signals are processed in terms of feedforward/feedbacks (or bottom-up/top-down) signaling. First, the data highlight to what extent the integration of different types of attentional signals depends on regions of the frontoparietal network: even for salience, that has been often thought to be processed solely in the occipital cortex (see Beck & Kastner, 2005; Yantis, 2005), I found that regions of the frontoparietal network were engaged (cf. effective connectivity in Experiment 1 and whole-brain analyses in Experiments 2 and 3). Second, my results suggest that the processing of salience relies also on feedback signaling (see also the use of the term "reentrant" in Martínez *et al.*, 1999), rather than solely bottom-up signaling from earlier to higher visual areas. Third, the results support previous works in favor of the bottom-up processing of statistical regularities (see Theeuwes, 2018, see Experiment 2 spatial

bias results in BA17 and functional connectivity results), but also nuance this claim by suggesting complementary mechanisms based on an interplay between the occipital cortex and PPC. Fourth, my three experiments highlight the interest of parceling the occipital areas as a function of their position in the visual hierarchy (see also Melloni *et al.*, 2012; Sprague *et al.*, 2018; Adam & Serences, 2021). With this, one can track how different signal-types are represented at different stages and how feedback/feedforward influences contribute at each level (see also descriptive analyses of the effect sizes).

5.3 Is there a priority map in the brain?

Based on the results of previous behavioral studies (e.g. Awh *et al.*, 2012; Chelazzi, Estocinova, *et al.*, 2014; Ferrante *et al.*, 2018), it is tempting to consider that there exists a spatial priority map in the brain that attributes attentional priority across the visual field (see Bisley & Mirpour, 2019). However, most recent experimental works (Melloni *et al.*, 2012; Sprague *et al.*, 2018; Adam & Serences, 2021) and reviews (Thompson & Bichot, 2005; Gottlieb, 2007; Ptak, 2012; Bisley & Mirpour, 2019; Anderson, 2021; Luck, Gaspelin, *et al.*, 2021) have introduced the idea that attentional priorities may rather be computed in multiple brain areas. The first key point in favor of this claim is that whole-brain imaging methods permitted to spatially map the visual field in several brain areas at the same time including the occipital cortex (Dumoulin & Wandell, 2008; Kay *et al.*, 2013), the posterior dorsal parietal cortex (Swisher *et al.*, 2007; Silver & Kastner, 2009; Jerde *et al.*, 2012; Mackey *et al.*, 2017) and the dorsal frontal cortex (Silver & Kastner, 2009; Jerde *et al.*, 2012; Mackey *et al.*, 2017). Secondly, there is extensive evidence that regions of the dorsal frontal and parietal cortices are involved in attentional control (see Corbetta & Shulman, 2002; Thompson & Bichot, 2005; Gottlieb, 2007; Ptak, 2012; Vossel, Geng, *et al.*, 2014). Several studies aimed to identify which areas of the dorsal frontoparietal network, that have both spatially-specific and attention-related responses, would best fit the role of a priority map. These works came to the conclusion that multiple regions both in dorsal frontal and parietal cortex code attentional priority albeit in a slightly different way (LIP in Gottlieb, 2007; PPC in Ptak, 2012; LIP, FEF in Bisley & Mirpour, 2019; see also Thompson & Bichot, 2005). As I mentioned in the introduction chapter, spatial maps in the occipital cortex have been mostly described as “saliency maps” (Itti & Koch, 2001; Chen *et al.*, 2016; Bisley & Mirpour, 2019) that do not integrate top-down factors. Nonetheless, it is now well acknowledged that also top-down signals modulate activity in the occipital cortex (Kastner, Pinsk, *et al.*, 1999; Melloni *et al.*, 2012; Sprague *et al.*, 2018; Won *et al.*, 2020; Adam & Serences, 2021; Zhang *et al.*, 2021, and the three experiments of this thesis). This, however, does not imply that occipital areas can be considered as visual priority maps: the “priority map-like” activity in these areas could be a result of computations performed in other regions (e.g. dorsal parietal and frontal areas; see Moore & Armstrong, 2003; Vossel,

Weidner, *et al.*, 2012). Accordingly, to be a priority map, a brain region has not only to represent attentional priorities across space, but also to integrate information coming from multiple sources of attentional signals.

In this thesis, I introduced a novel index to characterize spatial attentional priorities (i.e. the “spatial bias vectors”, cf. last section of the introduction) which, coupled with whole-brain, behavioral and connectivity analyses, allowed me to investigate how priorities are attributed across occipital areas. The spatial bias vectors quantify to what extent the overall quadrant-specific activity in the occipital cortex (separately for BA17/18/19) is biased towards the region of space that contains the task-relevant target. As part of the priority maps framework (see e.g. Chelazzi, Estocinova, *et al.*, 2014; Ferrante *et al.*, 2018), we predicted that the presentation of multiple attentional signals at the target location (e.g. a salient target, salient target display-condition; STD) would increase the spatial bias towards the target quadrant, reflecting higher overall attentional priority at the target location compared to a display with no salient item (i.e. homogeneous display-condition; HD). Across the three experiments, in most experimental conditions, I observed a spatial bias directed towards the target location in all BAs, which confirms that top-down guidance is represented along the entire visual hierarchy. However, across the experiments, when I considered the combination of these goal-directed signals with other sources of attention priority (statistical regularities and reward), I also observed patterns of activation in the occipital cortex that do not appear to directly fit predictions based on the priority maps framework. In figure 5.4, I attempt to summarize these effects and to reconcile the findings in the different experiments, by taking into account different mechanisms that may concur to setting the attention spatial priorities.

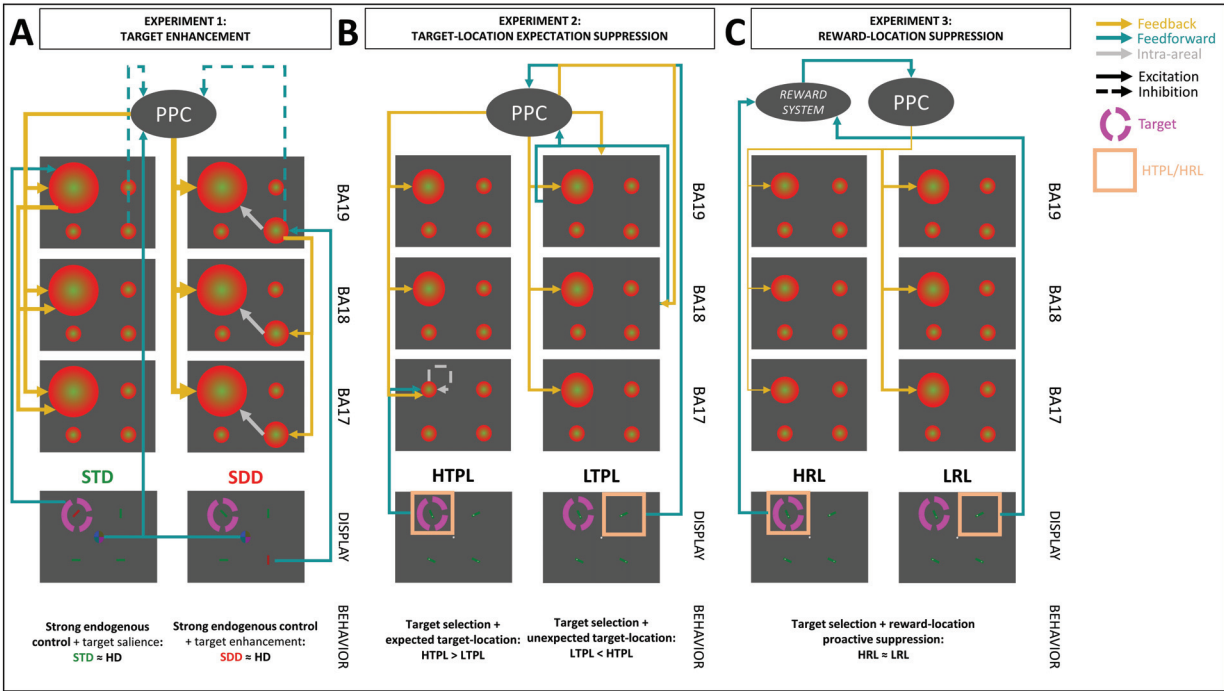


Figure 5.4: **Schema of the three main attentional prioritization mechanisms highlighted across the three experiments.**

The schema is extended from schemas in Corbetta & Shulman, 2002 and Luck, Gaspelin, *et al.*, 2021. The color-gradient circles represent the spatially-specific activations at the level of the three BAs, their size represents the activation gain. The arrows' thickness represents the connection strength. HTPL = high target-probability location; HRL = high-reward location. **A** - Target enhancement in Experiment 1. The blue lines from the display to the PPC indicate the setting of the target template (target orientation + target location). The blue arrows from the display to BA19 indicate the bottom-up contribution of the salience signal to responses in ROI_IN/ROI_OPP, while the orange arrows from BA19 to BA18 and BA17 indicate the re-entrant/feedback, salience-related signaling across the occipital hierarchy. The spatial incongruence between goal and salience signals in SDD is represented by thicker orange arrows (reactive target enhancement) from the PPC to the occipital target representations in SDD compared to STD (note: in Experiment 1, we highlighted this mechanism using effective connectivity only using the PPC and BA18 ROIs, but it is likely to be true also other BAs). Together, proactive and reactive enhancements lead to similar behavioral performances between all display-conditions. The additional dotted blue arrow from BA19 and PPC also refers to effective connectivity results, with an inhibitory influence of ROI_OPP on PPC (tested only on BA18 ROI_OPP, but assumed to be consistent across BAs). Note also the grey intra-areal arrow from ROI_OPP to ROI_IN in SDD but not in STD, also from our effective connectivity results (again, only tested in BA18, but assumed to be consistent across BAs). **B** - Sensory expectation suppression of the target representation in Experiment 2. Top-down target selection represented as in A. The grey dotted arrow at the target quadrant representation in BA17 represents the local sensory suppression occurring in the HTPL condition. In the HTPL condition, the blue arrow from the HTPL to ROI_IN in BA17 represents the mechanism inducing sensory suppression in BA17. In LTPL, the blue arrow from the display to the PPC refers to the higher PPC activation in LTPL than in HTPL. Orange and blue arrows between PPC and BA18/19 represent the functional connectivity results, with increased occipital-parietal interaction in LTPL. **C** - Reward signal suppression in Experiment 3. Top-down target selection represented as in A and B. Note: we did not specifically investigate interplays between the PPC and the reward system, these appear for illustrative purposes here. Blue arrows from the display to the reward system indicate the integration of the reward signal, which is assumed to be transmitted to the PPC also (see Bourgeois, Sterpenich, *et al.*, 2022). In our experiment, the reward signal was fully task-irrelevant, and was consequently suppressed (hence no significant difference of behavioral performances in HRL compared to LRL). Thinner orange arrows from the PPC to occipital BAs and smaller colored circles at the target representation in HRL compared to LRL represent the initial proactive suppression of the reward-related signal associated with the lower spatial bias in HRL compared to LRL.

In Experiment 1, I found that salience only marginally affected behavioral performances while it was reliably represented in occipital areas. In figure 5.4, I represented the mechanisms that may mediate this finding (cf. also previous sections of the Discussion). First, the 100% predictive cue induced a strong prioritization of the target location in all three BAs, via feed-back connectivity from fronto-parietal areas. In fig 5.3A this is represented by the blue arrow from the display-cues to the PPC, which then leads to strong feed-back signals from PPC to the 3 BAs (thick yellow arrows) and modulation

of the occipital spatial representations (large colored circles at the top-left location, corresponding to the cued/target location). These cueing/target quadrant enhancement effects are absent in Experiments 2-3 (cf. panels B-C). In addition, I found that additional mechanisms were at play depending on whether goal and salience signals were spatially-congruent (STD) or incongruent (SDD). These first concern an increase of the top-down target enhancement in SDD than in STD (thicker orange arrows from the PPC to the target-quadrant in SDD than in STD, panel A). Secondly, these mechanisms also comprise intra-occipital modulations, and most important, an enhancement/excitation from ROI_OPP to ROI_IN in SDD but not in STD. These local effects are represented by grey arrows in each of the occipital areas (panel A, SDD condition). Thus, multiple mechanisms would occur when goals and salience provide spatially-incongruent signals, involving both top-down control but also local interactions within the occipital cortex (see also Chapter 2). These complex patterns combining goal- and salience-related signals would be consistent with the fact that occipital regions comprise priority map features.

In Experiment 2, I found a reduced spatial bias towards the target location when the target was presented in the expected quadrant (HTPL) compared to when it was presented in an unexpected quadrant (LTPL), in BA17 only. According to our inter-regional connectivity analyses between the PPC and the three BAs (BA17, BA18, BA19, see figure 6 in Chapter 3), the effect in BA17 did not depend on interactions with the dorsal parietal cortex, suggesting a role of local computations in BA17 instead. In figure 5.4B, this is represented with a blue arrow from the HTPL display-quadrant to the target representation in the HTPL condition, and by the grey dotted arrow symbolizing local sensory expectation suppression mechanisms in BA17 (see sections above). At the behavioral level, participants were better at detecting the target in HTPL versus LTPL condition. First, this result shows that enhanced spatial priorities at the behavioral level do not merely translate into enhanced activity at the brain level: prioritization can also be reflected as a decrease of brain activity. In the context of Experiment 2, this can reflect a sharpening of the stimulus representation when it is expected, albeit the mechanisms of sensory suppression are still debated (Richter & de Lange, 2019; Alink & Blank, 2021). Second, the reduced spatial bias towards the target location for the HTPL condition occurring only in BA17 suggests that in Experiment 2, specifically BA17 coded statistical regularities in a spatially-specific way (see also Richter & de Lange, 2019; Adam & Serences, 2021 for results supporting this claim). However, inter-regional connectivity analyses revealed significant modulations of the coupling between the PPC and BA18/19 in LTPL compared to HTPL. This further indicates that the processing of spatial incongruence between goals (target location) and expectations (HTPL) relies on parietal-occipital functional interactions. In figure 5.4B, this is represented by the orange and blue arrows between BA18/19 and the PPC, in the LTPL condition. Together, these results show that computations in mul-

multiple areas are required to set attentional priorities leading to adaptive behavioral outputs.

In Experiment 3, I found that targets presented at the highly rewarded location (HRL) reduced the spatial bias compared to targets presented at the low reward locations (LRL). Crucially, no significant difference of frontoparietal or reward system activation was found between these two conditions. Based on the arguments provided in the two previous sections, I propose that the frontoparietal and reward systems were actually involved in the processing of the reward signals (cf. higher responses of the caudate nucleus when participants received 100 points versus 1 point, figure 5 in Chapter 4), but not in a sustained manner: on the long run, the suppression of the highly rewarded quadrant may have been encoded directly in the occipital cortex (cf. Geng & Duarte, 2021). In figure 5.4C, I illustrated this with interactions between the reward system and the PPC, that in turn resulted in a weaker top-down prioritization of the target quadrant in HRL than in LRL (cf. thin yellow arrows in panel C, HRL condition). Again, the results of Experiment 3 reveal that priorities are attributed on the basis of computations in multiple areas.

In this section, I attempted to explain how occipital areas compute attentional priorities. This would be in line with the notion according to which priority maps can be found in the occipital cortex, contrary to what was previously stated (see Bisley & Mirpour, 2019). I would like, however, to nuance this claim. Overall, my results suggest that attentional priorities are computed in different areas, mostly depending on the type of attentional signal at play (e.g. BA17 for expectations in Experiment 2; BA19 for salience in Experiments 1, 2 and 3, PPC for goals in Experiment 1). Actually, these different areas most likely compute only a part of the priorities (e.g. salience computations in saliency maps, see Itti & Koch, 2001; Veale *et al.*, 2017) that are not necessarily grouped into an “overall” priority map. However, the processing of priorities in all “partial” priority maps may be reflected at the level of the final behavioral performance (e.g. better performance when the target is salient than when it is not, in Experiments 2 and 3). In addition, depending on the employed stimuli/tasks, priorities may be computed in different ways. For example, BA17/V1 has been shown to be crucial for the computation of orientation-based salience, but not for other types of salience (Yoshida *et al.*, 2012), that may be processed in higher visual regions (Veale *et al.*, 2017, and see above).

5.4 New methodological challenges

The current results point out some limitations of the imaging/analysis methods that I used. Except for the effective connectivity analysis in Experiment 1, I did not directly assess the directionality on the inter-regional connectivity between the fronto-parietal network and the occipital cortex (i.e. feedback and/or feedforward). In addition, although dynamic causal modeling appeared in Experiment 1 as a very powerful tool (in particular

highlighting the target enhancement mechanism), it is noteworthy that these analyses have also important limitations. Ideally, the model space of the dynamic causal modeling analyses should have comprised multiple regions of the frontoparietal network (in all experiments) and of the reward system (in Experiment 3), plus the twelve occipital ROIs (4 quadrants x 3 BAs). Such analyses would have yielded virtually in infinity of a priori models to be tested and consequently an exponentially increasing computation time (see K. Stephan *et al.*, 2010). However, the definition of new model families as part of the DCM analyses could help resolving some of the outstanding questions that my studies raised. For example, the DCM model space in Experiment 1 comprised two families, one including the modulation of diffuse PPC-BA18 by the salience and the other including the modulation of only PPC-ROI_IN. In Experiment 2, another family of biologically plausible models could include only the modulation of intra-occipital connectivity by statistical regularities, so as to test the sensory expectation suppression hypothesis in a causal way. This family could also comprise models with and without self-connection/inhibition, accounting for the potential “sharpening” of the target representation in HTPL compared to LTPL. Moreover, complementary investigation tools, such as EEG (see Rashal *et al.*, 2022 as part of the MAC-Brain project, and see Martínez *et al.*, 1999; Martin *et al.*, 2019) and MEG that have a higher temporal resolution, would effectively contribute to assessing the cognitive mechanisms governing attentional priority attribution in the presence of multiple attentional signals.

5.5 General conclusions

The priority maps framework posits that spatial attentional abilities are governed by the coding - at the brain level - of attentional priorities in a spatially-specific manner. In my thesis, I tested whether these priorities could be reflected in occipital areas that contain well-organized representations of space, and what brain mechanisms govern the attribution of these priorities. I employed similar tasks across three experiments, where I manipulated different types of attentional signals. I computed a novel index called “spatial bias vector” that characterizes the overall bias of spatially distributed patterns of activity in the occipital cortex, and I conducted whole-brain and inter-regional connectivity analyses that allowed me to provide mechanistic explanations of the coding of attentional priorities in the occipital cortex. Across the three experiments, I showed that attention priorities are coded in the occipital cortex, but also that they do not systematically result in an increase of activity in the occipital region that represents the prioritized portion of the visual space. Rather, I revealed more complex mechanisms that govern the attribution of attentional priorities in the brain, via both enhancement and suppression mechanisms. These mechanisms entail local computations that take place locally in the occipital cortex, but also larger-scale interactions involving the connectivity between the occipital cortex and the fronto-parietal attention control network. Based on my multifaceted approach (behavior, whole-brain activations, spatial bias vectors, connectivity), I propose an updated view of the priority maps framework that comprises competitive interactions at multiple stages of visual processing.

Bibliography

1. Adam, K. C. & Serences, J. T. History Modulates Early Sensory Processing of Salient Distractors. *The Journal of Neuroscience* **41**, 8007–8022. ISSN: 0270-6474, 1529-2401. doi:[10.1523/JNEUROSCI.3099-20.2021](https://doi.org/10.1523/JNEUROSCI.3099-20.2021) (2021).
2. Alink, A., Schwiedrzik, C. M., Kohler, A., Singer, W. & Muckli, L. Stimulus Predictability Reduces Responses in Primary Visual Cortex. *Journal of Neuroscience* **30**, 2960–2966. ISSN: 0270-6474, 1529-2401. doi:[10.1523/JNEUROSCI.3730-10.2010](https://doi.org/10.1523/JNEUROSCI.3730-10.2010) (2010).
3. Alink, A. & Blank, H. Can expectation suppression be explained by reduced attention to predictable stimuli? *NeuroImage* **231**, 117824. ISSN: 10538119. doi:[10.1016/j.neuroimage.2021.117824](https://doi.org/10.1016/j.neuroimage.2021.117824) (2021).
4. Anderson, B. A., Laurent, P. A. & Yantis, S. Value-driven attentional capture. *Proceedings of the National Academy of Sciences* **108**, 10367–10371. ISSN: 0027-8424, 1091-6490. doi:[10.1073/pnas.1104047108](https://doi.org/10.1073/pnas.1104047108) (2011).
5. Anderson, B. A. The attention habit: how reward learning shapes attentional selection: The attention habit. *Annals of the New York Academy of Sciences* **1369**, 24–39. ISSN: 00778923. doi:[10.1111/nyas.12957](https://doi.org/10.1111/nyas.12957) (2016).
6. Anderson, B. A. Time to stop calling it attentional “capture” and embrace a mechanistic understanding of attentional priority. *Visual Cognition*, 1–4. ISSN: 1350-6285, 1464-0716. doi:[10.1080/13506285.2021.1892894](https://doi.org/10.1080/13506285.2021.1892894) (2021).
7. Anderson, B. A., Kuwabara, H., *et al.* Linking dopaminergic reward signals to the development of attentional bias: A positron emission tomographic study. *NeuroImage* **157**, 27–33. ISSN: 10538119. doi:[10.1016/j.neuroimage.2017.05.062](https://doi.org/10.1016/j.neuroimage.2017.05.062) (2017).
8. Anderson, B. A., Laurent, P. A. & Yantis, S. Value-driven attentional priority signals in human basal ganglia and visual cortex. *Brain Research* **1587**, 88–96. ISSN: 00068993. doi:[10.1016/j.brainres.2014.08.062](https://doi.org/10.1016/j.brainres.2014.08.062) (2014).
9. Awh, E., Belopolsky, A. V. & Theeuwes, J. Top-down versus bottom-up attentional control: a failed theoretical dichotomy. *Trends in Cognitive Sciences* **16**, 437–443. ISSN: 13646613. doi:[10.1016/j.tics.2012.06.010](https://doi.org/10.1016/j.tics.2012.06.010) (2012).
10. Baddeley, A. Working memory. *Current Biology* **20**, R136–R140. ISSN: 09609822. doi:[10.1016/j.cub.2009.12.014](https://doi.org/10.1016/j.cub.2009.12.014) (2010).
11. Bates, D., Mächler, M., Bolker, B. & Walker, S. Fitting Linear Mixed-Effects Models Using **lme4**. *Journal of Statistical Software* **67**. ISSN: 1548-7660. doi:[10.18637/jss.v067.i01](https://doi.org/10.18637/jss.v067.i01) (2015).
12. Beck, D. M. & Kastner, S. Stimulus context modulates competition in human extrastriate cortex. *Nature Neuroscience* **8**, 1110–1116. ISSN: 1097-6256, 1546-1726. doi:[10.1038/nn1501](https://doi.org/10.1038/nn1501) (2005).

13. Beffara, B. *et al.* Dynamic causal interactions between occipital and parietal cortex explain how endogenous spatial attention and stimulus-driven salience jointly shape the distribution of processing priorities in 2D visual space. *NeuroImage* **255**, 119206. ISSN: 10538119. doi:[10.1016/j.neuroimage.2022.119206](https://doi.org/10.1016/j.neuroimage.2022.119206) (2022).
14. Belopolsky, A. V., Zwaan, L., Theeuwes, J. & Kramer, A. F. The size of an attentional window modulates attentional capture by color singletons. *Psychonomic Bulletin & Review* **14**, 934–938. ISSN: 1069-9384, 1531-5320. doi:[10.3758/BF03194124](https://doi.org/10.3758/BF03194124) (2007).
15. Berger, A., Henik, A. & Rafal, R. Competition Between Endogenous and Exogenous Orienting of Visual Attention. *Journal of Experimental Psychology: General* **134**, 207–221. ISSN: 1939-2222, 0096-3445. doi:[10.1037/0096-3445.134.2.207](https://doi.org/10.1037/0096-3445.134.2.207) (2005).
16. Betz, T., Wilming, N., Bogler, C., Haynes, J.-D. & Konig, P. Dissociation between saliency signals and activity in early visual cortex. *Journal of Vision* **13**, 6–6. ISSN: 1534-7362. doi:[10.1167/13.14.6](https://doi.org/10.1167/13.14.6) (2013).
17. Bisley, J. W. & Mirpour, K. The neural instantiation of a priority map. *Current Opinion in Psychology* **29**, 108–112. ISSN: 2352250X. doi:[10.1016/j.copsyc.2019.01.002](https://doi.org/10.1016/j.copsyc.2019.01.002) (2019).
18. Bles, M., Schwarzbach, J., De Weerd, P., Goebel, R. & Jansma, B. M. Receptive field size-dependent attention effects in simultaneously presented stimulus displays. *NeuroImage* **30**, 506–511. ISSN: 10538119. doi:[10.1016/j.neuroimage.2005.09.042](https://doi.org/10.1016/j.neuroimage.2005.09.042) (2006).
19. Bourgeois, A., Chelazzi, L. & Vuilleumier, P. in *Progress in Brain Research* 325–342 (Elsevier, 2016). ISBN: 978-0-444-63701-7. doi:[10.1016/bs.pbr.2016.06.004](https://doi.org/10.1016/bs.pbr.2016.06.004).
20. Bourgeois, A., Sterpenich, V., Iannotti, G. R. & Vuilleumier, P. Reward-driven modulation of spatial attention in the human frontal eye-field. *NeuroImage* **247**, 118846. ISSN: 10538119. doi:[10.1016/j.neuroimage.2021.118846](https://doi.org/10.1016/j.neuroimage.2021.118846) (2022).
21. Bowling, J. T., Friston, K. J. & Hopfinger, J. B. Top-down versus bottom-up attention differentially modulate frontal–parietal connectivity. *Human Brain Mapping* **41**, 928–942. ISSN: 1065-9471, 1097-0193. doi:[10.1002/hbm.24850](https://doi.org/10.1002/hbm.24850) (2020).
22. Brázdil, M., Mikl, M., Mareček, R., Krupa, P. & Rektor, I. Effective connectivity in target stimulus processing: A dynamic causal modeling study of visual oddball task. *NeuroImage* **35**, 827–835. ISSN: 10538119. doi:[10.1016/j.neuroimage.2006.12.020](https://doi.org/10.1016/j.neuroimage.2006.12.020) (2007).
23. Brefczynski, J. A. & DeYoe, E. A. A physiological correlate of the ‘spotlight’ of visual attention. *Nature Neuroscience* **2**, 370–374. ISSN: 1097-6256, 1546-1726. doi:[10.1038/7280](https://doi.org/10.1038/7280) (1999).
24. Buchel, C. Modulation of connectivity in visual pathways by attention: cortical interactions evaluated with structural equation modelling and fMRI. *Cerebral Cortex* **7**, 768–778. ISSN: 14602199. doi:[10.1093/cercor/7.8.768](https://doi.org/10.1093/cercor/7.8.768) (1997).
25. Buschman, T. J. & Miller, E. K. Top-Down Versus Bottom-Up Control of Attention in the Prefrontal and Posterior Parietal Cortices. *Science* **315**, 1860–1862. ISSN: 0036-8075, 1095-9203. doi:[10.1126/science.1138071](https://doi.org/10.1126/science.1138071) (2007).
26. Buschsulte, A. *et al.* Reward- and Attention-related Biasing of Sensory Selection in Visual Cortex. *Journal of Cognitive Neuroscience* **26**, 1049–1065. ISSN: 0898-929X, 1530-8898. doi:[10.1162/jocn_a_00539](https://doi.org/10.1162/jocn_a_00539) (2014).
27. Chelazzi, L., Estocinova, J., *et al.* Altering Spatial Priority Maps via Reward-Based Learning. *Journal of Neuroscience* **34**, 8594–8604. ISSN: 0270-6474, 1529-2401. doi:[10.1523/JNEUROSCI.0277-14.2014](https://doi.org/10.1523/JNEUROSCI.0277-14.2014) (2014).

28. Chelazzi, L., Della Libera, C., Sani, I. & Santandrea, E. Neural basis of visual selective attention: Visual selective attention. *Wiley Interdisciplinary Reviews: Cognitive Science* **2**, 392–407. ISSN: 19395078. doi:[10.1002/wcs.117](https://doi.org/10.1002/wcs.117) (2011).
29. Chelazzi, L., Duncan, J., Miller, E. K. & Desimone, R. Responses of Neurons in Inferior Temporal Cortex During Memory-Guided Visual Search. *Journal of Neurophysiology* **80**, 2918–2940. ISSN: 0022-3077, 1522-1598. doi:[10.1152/jn.1998.80.6.2918](https://doi.org/10.1152/jn.1998.80.6.2918) (1998).
30. Chelazzi, L., Marini, F., Pascucci, D. & Turatto, M. Getting rid of visual distractors: the why, when, how, and where. *Current Opinion in Psychology* **29**, 135–147. ISSN: 2352250X. doi:[10.1016/j.copsyc.2019.02.004](https://doi.org/10.1016/j.copsyc.2019.02.004) (2019).
31. Chelazzi, L., Perlato, A., Santandrea, E. & Della Libera, C. Rewards teach visual selective attention. *Vision Research* **85**, 58–72. ISSN: 00426989. doi:[10.1016/j.visres.2012.12.005](https://doi.org/10.1016/j.visres.2012.12.005) (2013).
32. Chen, C., Zhang, X., Wang, Y., Zhou, T. & Fang, F. Neural activities in V1 create the bottom-up saliency map of natural scenes. *Experimental Brain Research* **234**, 1769–1780. ISSN: 0014-4819, 1432-1106. doi:[10.1007/s00221-016-4583-y](https://doi.org/10.1007/s00221-016-4583-y) (2016).
33. Chica, A. B., Bartolomeo, P. & Valero-Cabre, A. Dorsal and Ventral Parietal Contributions to Spatial Orienting in the Human Brain. *Journal of Neuroscience* **31**, 8143–8149. ISSN: 0270-6474, 1529-2401. doi:[10.1523/JNEUROSCI.5463-10.2010](https://doi.org/10.1523/JNEUROSCI.5463-10.2010) (2011).
34. Chica, A. B., Bartolomeo, P. & Lupiáñez, J. Two cognitive and neural systems for endogenous and exogenous spatial attention. *Behavioural Brain Research* **237**, 107–123. ISSN: 01664328. doi:[10.1016/j.bbr.2012.09.027](https://doi.org/10.1016/j.bbr.2012.09.027) (2013).
35. Clark, C. W. The behavioral ecology of a cognitive constraint: limited attention. *Behavioral Ecology* **14**, 151–156. ISSN: 14657279. doi:[10.1093/beheco/14.2.151](https://doi.org/10.1093/beheco/14.2.151) (2003).
36. Corbetta, M., Kincade, J. M., Ollinger, J. M., McAvoy, M. P. & Shulman, G. L. Voluntary orienting is dissociated from target detection in human posterior parietal cortex. *Nature Neuroscience* **3**, 292–297. ISSN: 1097-6256, 1546-1726. doi:[10.1038/73009](https://doi.org/10.1038/73009) (2000).
37. Corbetta, M., Patel, G. & Shulman, G. L. The Reorienting System of the Human Brain: From Environment to Theory of Mind. *Neuron* **58**, 306–324. ISSN: 08966273. doi:[10.1016/j.neuron.2008.04.017](https://doi.org/10.1016/j.neuron.2008.04.017) (2008).
38. Corbetta, M. & Shulman, G. L. Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience* **3**, 201–215. ISSN: 1471-003X, 1471-0048. doi:[10.1038/nrn755](https://doi.org/10.1038/nrn755) (2002).
39. De Groot, F., Huettig, F. & Olivers, C. N. L. When meaning matters: The temporal dynamics of semantic influences on visual attention. *Journal of Experimental Psychology: Human Perception and Performance* **42**, 180–196. ISSN: 1939-1277, 0096-1523. doi:[10.1037/xhp0000102](https://doi.org/10.1037/xhp0000102) (2016).
40. Desimone, R. Visual attention mediated by biased competition in extrastriate visual cortex. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* **353** (eds Humphreys, G. W., Duncan, J. & Treisman, A.) 1245–1255. ISSN: 0962-8436, 1471-2970. doi:[10.1098/rstb.1998.0280](https://doi.org/10.1098/rstb.1998.0280) (1998).
41. Desimone, R. & Duncan, J. Neural mechanisms of selective visual attention. *Annual Review of Neuroscience* **18**, 193–222. ISSN: 0147-006X. doi:[10.1146/annurev.ne.18.030195.001205](https://doi.org/10.1146/annurev.ne.18.030195.001205) (1995).
42. Desimone, R. Visual attention mediated by biased competition in extrastriate visual cortex. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* **353** (eds Humphreys, G. W., Duncan, J. & Treisman, A.) 1245–1255. ISSN: 0962-8436, 1471-2970. doi:[10.1098/rstb.1998.0280](https://doi.org/10.1098/rstb.1998.0280) (1998).

43. Desseilles, M. *et al.* Depression alters “top-down” visual attention: A dynamic causal modeling comparison between depressed and healthy subjects. *NeuroImage* **54**, 1662–1668. ISSN: 10538119. doi:10.1016/j.neuroimage.2010.08.061 (2011).
44. DiQuattro, N. E. & Geng, J. J. Contextual Knowledge Configures Attentional Control Networks. *Journal of Neuroscience* **31**, 18026–18035. ISSN: 0270-6474, 1529-2401. doi:10.1523/JNEUROSCI.4040-11.2011 (2011).
45. DiQuattro, N. E., Sawaki, R. & Geng, J. J. Effective Connectivity During Feature-Based Attentional Capture: Evidence Against the Attentional Reorienting Hypothesis of TPJ. *Cerebral Cortex* **24**, 3131–3141. ISSN: 1047-3211, 1460-2199. doi:10.1093/cercor/bht172 (2014).
46. Doricchi, F., Macci, E., Silvetti, M. & Macaluso, E. Neural Correlates of the Spatial and Expectancy Components of Endogenous and Stimulus-Driven Orienting of Attention in the Posner Task. *Cerebral Cortex* **20**, 1574–1585. ISSN: 1047-3211, 1460-2199. doi:10.1093/cercor/bhp215 (2010).
47. Downar, J., Crawley, A. P., Mikulis, D. J. & Davis, K. D. A Cortical Network Sensitive to Stimulus Salience in a Neutral Behavioral Context Across Multiple Sensory Modalities. *Journal of Neurophysiology* **87**, 615–620. ISSN: 0022-3077, 1522-1598. doi:10.1152/jn.00636.2001 (2002).
48. Driver, J. A selective review of selective attention research from the past century. *British Journal of Psychology* **92**, 53–78. ISSN: 00071269. doi:10.1348/000712601162103 (2001).
49. Dukas, R. Limited attention: the constraint underlying search image. *Behavioral Ecology* **12**, 192–199. ISSN: 14657279. doi:10.1093/beheco/12.2.192 (2001).
50. Dukas, R. The cost of limited attention in blue jays. *Behavioral Ecology* **11**, 502–506. ISSN: 14657279. doi:10.1093/beheco/11.5.502 (2000).
51. Dukas, R. Causes and Consequences of Limited Attention. *Brain, Behavior and Evolution* **63**, 197–210. ISSN: 1421-9743, 0006-8977. doi:10.1159/000076781 (2004).
52. Dumoulin, S. O. & Wandell, B. A. Population receptive field estimates in human visual cortex. *NeuroImage* **39**, 647–660. ISSN: 10538119. doi:10.1016/j.neuroimage.2007.09.034 (2008).
53. Duncan, J., Treisman, A. & Desimone, R. Visual attention mediated by biased competition in extrastriate visual cortex. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* **353** (ed Humphreys, G. W.) 1245–1255. ISSN: 0962-8436, 1471-2970. doi:10.1098/rstb.1998.0280 (1998).
54. Duncan, J. Converging levels of analysis in the cognitive neuroscience of visual attention. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* **353** (eds Humphreys, G. W., Duncan, J. & Treisman, A.) 1307–1317. ISSN: 0962-8436, 1471-2970. doi:10.1098/rstb.1998.0285 (1998).
55. Efron, R. in *Proceedings of the Boston Colloquium for the Philosophy of Science 1966/1968* (eds Cohen, R. S. & Wartofsky, M. W.) Series Title: Boston Studies in the Philosophy of Science, 137–173 (Springer Netherlands, Dordrecht, 1969). ISBN: 978-94-010-3380-0 978-94-010-3378-7. doi:10.1007/978-94-010-3378-7_4.
56. Egeth, H. E. & Yantis, S. VISUAL ATTENTION: Control, Representation, and Time Course. *Annual Review of Psychology* **48**, 269–297. ISSN: 0066-4308, 1545-2085. doi:10.1146/annurev.psych.48.1.269 (1997).
57. Engel, S. Retinotopic organization in human visual cortex and the spatial precision of functional MRI. *Cerebral Cortex* **7**, 181–192. ISSN: 14602199. doi:10.1093/cercor/7.2.181 (1997).

58. Ferrante, O. *et al.* Altering spatial priority maps via statistical learning of target selection and distractor filtering. *Cortex* **102**, 67–95. ISSN: 00109452. doi:[10.1016/j.cortex.2017.09.027](https://doi.org/10.1016/j.cortex.2017.09.027) (2018).
59. Folk, C. L., Remington, R. W. & Johnston, J. C. Involuntary covert orienting is contingent on attentional control settings. *Journal of Experimental Psychology: Human Perception and Performance* **18**, 1030–1044. ISSN: 1939-1277, 0096-1523. doi:[10.1037/0096-1523.18.4.1030](https://doi.org/10.1037/0096-1523.18.4.1030) (1992).
60. Friston, K., Buechel, C., *et al.* Psychophysiological and Modulatory Interactions in Neuroimaging. *NeuroImage* **6**, 218–229. ISSN: 10538119. doi:[10.1006/nimg.1997.0291](https://doi.org/10.1006/nimg.1997.0291) (1997).
61. Friston, K., Harrison, L. & Penny, W. Dynamic causal modelling. *NeuroImage* **19**, 1273–1302. ISSN: 10538119. doi:[10.1016/S1053-8119\(03\)00202-7](https://doi.org/10.1016/S1053-8119(03)00202-7) (2003).
62. Friston, K., Mattout, J., Trujillo-Barreto, N., Ashburner, J. & Penny, W. Variational free energy and the Laplace approximation. *NeuroImage* **34**, 220–234. ISSN: 10538119. doi:[10.1016/j.neuroimage.2006.08.035](https://doi.org/10.1016/j.neuroimage.2006.08.035) (2007).
63. Gandhi, S. P., Heeger, D. J. & Boynton, G. M. Spatial attention affects brain activity in human primary visual cortex. *Proceedings of the National Academy of Sciences* **96**, 3314–3319. ISSN: 0027-8424, 1091-6490. doi:[10.1073/pnas.96.6.3314](https://doi.org/10.1073/pnas.96.6.3314) (1999).
64. Gaspelin, N., Leonard, C. J. & Luck, S. J. Suppression of overt attentional capture by salient-but-irrelevant color singletons. *Attention, Perception, & Psychophysics* **79**, 45–62. ISSN: 1943-3921, 1943-393X. doi:[10.3758/s13414-016-1209-1](https://doi.org/10.3758/s13414-016-1209-1) (2017).
65. Gaspelin, N. & Luck, S. J. Distinguishing among potential mechanisms of singleton suppression. *Journal of Experimental Psychology: Human Perception and Performance* **44**, 626–644. ISSN: 1939-1277, 0096-1523. doi:[10.1037/xhp0000484](https://doi.org/10.1037/xhp0000484) (2018).
66. Geng, J. J. & DiQuattro, N. E. Attentional capture by a perceptually salient non-target facilitates target processing through inhibition and rapid rejection. *Journal of Vision* **10**, 5–5. ISSN: 1534-7362. doi:[10.1167/10.6.5](https://doi.org/10.1167/10.6.5) (2010).
67. Geng, J. J. Attentional Mechanisms of Distractor Suppression. *Current Directions in Psychological Science* **23**, 147–153. ISSN: 0963-7214, 1467-8721. doi:[10.1177/0963721414525780](https://doi.org/10.1177/0963721414525780) (2014).
68. Geng, J. J. & Duarte, S. E. Unresolved issues in distractor suppression: Proactive and reactive mechanisms, implicit learning, and naturalistic distraction. *Visual Cognition* **29**, 608–613. ISSN: 1350-6285, 1464-0716. doi:[10.1080/13506285.2021.1928806](https://doi.org/10.1080/13506285.2021.1928806) (2021).
69. Gibson, B. S. & Kingstone, A. Visual Attention and the Semantics of Space: Beyond Central and Peripheral Cues. *Psychological Science* **17**, 622–627. ISSN: 0956-7976, 1467-9280. doi:[10.1111/j.1467-9280.2006.01754.x](https://doi.org/10.1111/j.1467-9280.2006.01754.x) (2006).
70. Gitelman, D. R., Penny, W. D., Ashburner, J. & Friston, K. J. Modeling regional and psychophysiological interactions in fMRI: the importance of hemodynamic deconvolution. *NeuroImage* **19**, 200–207. ISSN: 10538119. doi:[10.1016/S1053-8119\(03\)00058-2](https://doi.org/10.1016/S1053-8119(03)00058-2) (2003).
71. Goldberg, M. C., Maurer, D. & Lewis, T. L. Developmental changes in attention: the effects of endogenous cueing and of distractors. *Developmental Science* **4**, 209–219. ISSN: 1363-755X, 1467-7687. doi:[10.1111/1467-7687.00166](https://doi.org/10.1111/1467-7687.00166) (2001).
72. Gottlieb, J. From Thought to Action: The Parietal Cortex as a Bridge between Perception, Action, and Cognition. *Neuron* **53**, 9–16. ISSN: 08966273. doi:[10.1016/j.neuron.2006.12.009](https://doi.org/10.1016/j.neuron.2006.12.009) (2007).
73. Grahek, I., Schettino, A., Koster, E. H. & Andersen, S. K. *Dynamic interplay between reward and voluntary attention determines stimulus processing in visual cortex* preprint (Neuroscience, 2021). doi:[10.1101/2021.06.17.448788](https://doi.org/10.1101/2021.06.17.448788).

74. Haynes, J.-D., Tregellas, J. & Rees, G. Attentional integration between anatomically distinct stimulus representations in early visual cortex. *Proceedings of the National Academy of Sciences* **102**, 14925–14930. ISSN: 0027-8424, 1091-6490. doi:[10.1073/pnas.0501684102](https://doi.org/10.1073/pnas.0501684102) (2005).
75. Heinemann, L., Kleinschmidt, A. & Müller, N. G. Exploring BOLD Changes during Spatial Attention in Non-Stimulated Visual Cortex. *PLoS ONE* **4** (ed Whitney, D.) e5560. ISSN: 1932-6203. doi:[10.1371/journal.pone.0005560](https://doi.org/10.1371/journal.pone.0005560) (2009).
76. Heinze, H. J. *et al.* Combined spatial and temporal imaging of brain activity during visual selective attention in humans. *Nature* **372**, 543–546. ISSN: 0028-0836. doi:[10.1038/372543a0](https://doi.org/10.1038/372543a0) (1994).
77. Hickey, C. & Peelen, M. V. Neural Mechanisms of Incentive Saliency in Naturalistic Human Vision. *Neuron* **85**, 512–518. ISSN: 08966273. doi:[10.1016/j.neuron.2014.12.049](https://doi.org/10.1016/j.neuron.2014.12.049) (2015).
78. Hodsoll, J., Mevorach, C. & Humphreys, G. W. Driven to Less Distraction: rTMS of the Right Parietal Cortex Reduces Attentional Capture in Visual Search. *Cerebral Cortex* **19**, 106–114. ISSN: 1047-3211, 1460-2199. doi:[10.1093/cercor/bhn070](https://doi.org/10.1093/cercor/bhn070) (2009).
79. Hommel, B. *et al.* No one knows what attention is. *Attention, Perception, & Psychophysics* **81**, 2288–2303. ISSN: 1943-3921, 1943-393X. doi:[10.3758/s13414-019-01846-w](https://doi.org/10.3758/s13414-019-01846-w) (2019).
80. Hopf, J.-M. *et al.* Popout modulates focal attention in the primary visual cortex. *NeuroImage* **22**, 574–582. ISSN: 10538119. doi:[10.1016/j.neuroimage.2004.01.031](https://doi.org/10.1016/j.neuroimage.2004.01.031) (2004).
81. Hubel, D. H. & Wiesel, T. N. Receptive fields of single neurones in the cat's striate cortex. *The Journal of Physiology* **148**, 574–591. ISSN: 00223751. doi:[10.1113/jphysiol.1959.sp006308](https://doi.org/10.1113/jphysiol.1959.sp006308) (1959).
82. Ibos, G., Duhamel, J.-R. & Ben Hamed, S. A Functional Hierarchy within the Parietofrontal Network in Stimulus Selection and Attention Control. *Journal of Neuroscience* **33**, 8359–8369. ISSN: 0270-6474, 1529-2401. doi:[10.1523/JNEUROSCI.4058-12.2013](https://doi.org/10.1523/JNEUROSCI.4058-12.2013) (2013).
83. Indovina, I. & Macaluso, E. Dissociation of Stimulus Relevance and Saliency Factors during Shifts of Visuospatial Attention. *Cerebral Cortex* **17**, 1701–1711. ISSN: 1460-2199, 1047-3211. doi:[10.1093/cercor/bh1081](https://doi.org/10.1093/cercor/bh1081) (2007).
84. Itti, L. & Koch, C. Computational modelling of visual attention. *Nature Reviews Neuroscience* **2**, 194–203. ISSN: 1471-003X, 1471-0048. doi:[10.1038/35058500](https://doi.org/10.1038/35058500) (2001).
85. James, W. *The principles of psychology: in two volumes. Vol. 1* Facsim. of ed. New York, Henry Holt, 1890. 689 pp. ISBN: 978-0-486-20381-2 (Dover, New York, 1995).
86. Jerde, T. A., Merriam, E. P., Riggall, A. C., Hedges, J. H. & Curtis, C. E. Prioritized Maps of Space in Human Frontoparietal Cortex. *Journal of Neuroscience* **32**, 17382–17390. ISSN: 0270-6474, 1529-2401. doi:[10.1523/JNEUROSCI.3810-12.2012](https://doi.org/10.1523/JNEUROSCI.3810-12.2012) (2012).
87. Kastner, S. Mechanisms of Directed Attention in the Human Extrastriate Cortex as Revealed by Functional MRI. *Science* **282**, 108–111. doi:[10.1126/science.282.5386.108](https://doi.org/10.1126/science.282.5386.108) (1998).
88. Kastner, S., De Weerd, P., Desimone, R. & Ungerleider, L. G. Mechanisms of directed attention in the human extrastriate cortex as revealed by functional MRI. *Science (New York, N.Y.)* **282**, 108–111. ISSN: 0036-8075. doi:[10.1126/science.282.5386.108](https://doi.org/10.1126/science.282.5386.108) (1998).
89. Kastner, S., De Weerd, P., Pinsk, M. A., *et al.* Modulation of Sensory Suppression: Implications for Receptive Field Sizes in the Human Visual Cortex. *Journal of Neurophysiology* **86**, 1398–1411. ISSN: 0022-3077, 1522-1598. doi:[10.1152/jn.2001.86.3.1398](https://doi.org/10.1152/jn.2001.86.3.1398) (2001).
90. Kastner, S., Pinsk, M. A., De Weerd, P., Desimone, R. & Ungerleider, L. G. Increased Activity in Human Visual Cortex during Directed Attention in the Absence of Visual Stimulation. *Neuron* **22**, 751–761. ISSN: 08966273. doi:[10.1016/S0896-6273\(00\)80734-5](https://doi.org/10.1016/S0896-6273(00)80734-5) (1999).

91. Kay, K. N., Winawer, J., Mezer, A. & Wandell, B. A. Compressive spatial summation in human visual cortex. *Journal of Neurophysiology* **110**, 481–494. ISSN: 0022-3077, 1522-1598. doi:[10.1152/jn.00105.2013](https://doi.org/10.1152/jn.00105.2013) (2013).
92. Kim, H. & Anderson, B. A. Combined influence of valence and statistical learning on the control of attention: Evidence for independent sources of bias. *Cognition* **208**, 104554. ISSN: 00100277. doi:[10.1016/j.cognition.2020.104554](https://doi.org/10.1016/j.cognition.2020.104554) (2021).
93. Kincade, J. M. An Event-Related Functional Magnetic Resonance Imaging Study of Voluntary and Stimulus-Driven Orienting of Attention. *Journal of Neuroscience* **25**, 4593–4604. ISSN: 0270-6474, 1529-2401. doi:[10.1523/JNEUROSCI.0236-05.2005](https://doi.org/10.1523/JNEUROSCI.0236-05.2005) (2005).
94. Klein, J. T., Shepherd, S. V. & Platt, M. L. Social Attention and the Brain. *Current Biology* **19**, R958–R962. ISSN: 09609822. doi:[10.1016/j.cub.2009.08.010](https://doi.org/10.1016/j.cub.2009.08.010) (2009).
95. Koch, C. & Ullman, S. Shifts in selective visual attention: towards the underlying neural circuitry. *Human Neurobiology* **4**, 219–227. ISSN: 0721-9075 (1985).
96. Lauritzen, T. Z., D’Esposito, M., Heeger, D. J. & Silver, M. A. Top-down flow of visual spatial attention signals from parietal to occipital cortex. *Journal of Vision* **9**, 18–18. ISSN: 1534-7362. doi:[10.1167/9.13.18](https://doi.org/10.1167/9.13.18) (2009).
97. Leber, A. B. & Egeth, H. E. It’s under control: Top-down search strategies can override attentional capture. *Psychonomic Bulletin & Review* **13**, 132–138. ISSN: 1069-9384, 1531-5320. doi:[10.3758/BF03193824](https://doi.org/10.3758/BF03193824) (2006).
98. Leber, A. B., Gwinn, R. E., Hong, Y. & O’Toole, R. J. Implicitly learned suppression of irrelevant spatial locations. *Psychonomic Bulletin & Review* **23**, 1873–1881. ISSN: 1069-9384, 1531-5320. doi:[10.3758/s13423-016-1065-y](https://doi.org/10.3758/s13423-016-1065-y) (2016).
99. Li, Z. A saliency map in primary visual cortex. *Trends in Cognitive Sciences* **6**, 9–16. ISSN: 1879-307X. doi:[10.1016/s1364-6613\(00\)01817-9](https://doi.org/10.1016/s1364-6613(00)01817-9) (2002).
100. Luck, S. J. Multiple mechanisms of visual-spatial attention: recent evidence from human electrophysiology. *Behavioural Brain Research*, 11 (1995).
101. Luck, S. J., Chelazzi, L., Hillyard, S. A. & Desimone, R. Neural Mechanisms of Spatial Selective Attention in Areas V1, V2, and V4 of Macaque Visual Cortex. *Journal of Neurophysiology* **77**, 24–42. ISSN: 0022-3077, 1522-1598. doi:[10.1152/jn.1997.77.1.24](https://doi.org/10.1152/jn.1997.77.1.24) (1997).
102. Luck, S. J., Gaspelin, N., Folk, C. L., Remington, R. W. & Theeuwes, J. Progress toward resolving the attentional capture debate. *Visual Cognition* **29**, 1–21. ISSN: 1350-6285, 1464-0716. doi:[10.1080/13506285.2020.1848949](https://doi.org/10.1080/13506285.2020.1848949) (2021).
103. Lupyan, G. Changing What You See by Changing What You Know: The Role of Attention. *Frontiers in Psychology* **8**, 553. ISSN: 1664-1078. doi:[10.3389/fpsyg.2017.00553](https://doi.org/10.3389/fpsyg.2017.00553) (2017).
104. Macaluso, E. & Doricchi, F. Attention and predictions: control of spatial attention beyond the endogenous-exogenous dichotomy. *Frontiers in Human Neuroscience* **7**. ISSN: 1662-5161. doi:[10.3389/fnhum.2013.00685](https://doi.org/10.3389/fnhum.2013.00685) (2013).
105. Mackey, W. E., Winawer, J. & Curtis, C. E. Visual field map clusters in human frontoparietal cortex. *eLife* **6**, e22974. ISSN: 2050-084X. doi:[10.7554/eLife.22974](https://doi.org/10.7554/eLife.22974) (2017).
106. Maquestiaux, F. *Psychologie de l’attention* 2e éd. ISBN: 978-2-8073-0736-0 (De Boeck supérieur, Louvain-la-Neuve (Belgique), 2017).
107. Martin, A. B. *et al.* Temporal Dynamics and Response Modulation across the Human Visual System in a Spatial Attention Task: An ECoG Study. *The Journal of Neuroscience* **39**, 333–352. ISSN: 0270-6474, 1529-2401. doi:[10.1523/JNEUROSCI.1889-18.2018](https://doi.org/10.1523/JNEUROSCI.1889-18.2018) (2019).

108. Martínez, A. *et al.* Involvement of striate and extrastriate visual cortical areas in spatial attention. *Nature Neuroscience* **2**, 364–369. ISSN: 1097-6256, 1546-1726. doi:[10.1038/7274](https://doi.org/10.1038/7274) (1999).
109. Mazer, J. A. & Gallant, J. L. Goal-related activity in V4 during free viewing visual search. Evidence for a ventral stream visual salience map. *Neuron* **40**, 1241–1250. ISSN: 0896-6273. doi:[10.1016/S0896-6273\(03\)00764-5](https://doi.org/10.1016/S0896-6273(03)00764-5) (2003).
110. McLaren, D. G., Ries, M. L., Xu, G. & Johnson, S. C. A generalized form of context-dependent psychophysiological interactions (gPPI): A comparison to standard approaches. *NeuroImage* **61**, 1277–1286. ISSN: 10538119. doi:[10.1016/j.neuroimage.2012.03.068](https://doi.org/10.1016/j.neuroimage.2012.03.068) (2012).
111. Melloni, L., van Leeuwen, S., Alink, A. & Müller, N. G. Interaction between Bottom-up Saliency and Top-down Control: How Saliency Maps Are Created in the Human Brain. *Cerebral Cortex* **22**, 2943–2952. ISSN: 1460-2199, 1047-3211. doi:[10.1093/cercor/bhr384](https://doi.org/10.1093/cercor/bhr384) (2012).
112. Mevorach, C., Humphreys, G. W. & Shalev, L. Opposite biases in salience-based selection for the left and right posterior parietal cortex. *Nature Neuroscience* **9**, 740–742. ISSN: 1097-6256, 1546-1726. doi:[10.1038/mn1709](https://doi.org/10.1038/mn1709) (2006).
113. Miller, E. K., Erickson, C. A. & Desimone, R. Neural Mechanisms of Visual Working Memory in Prefrontal Cortex of the Macaque. *The Journal of Neuroscience* **16**, 5154–5167. ISSN: 0270-6474, 1529-2401. doi:[10.1523/JNEUROSCI.16-16-05154.1996](https://doi.org/10.1523/JNEUROSCI.16-16-05154.1996) (1996).
114. Moore, T. & Armstrong, K. M. Selective gating of visual signals by microstimulation of frontal cortex. *Nature* **421**, 370–373. ISSN: 0028-0836, 1476-4687. doi:[10.1038/nature01341](https://doi.org/10.1038/nature01341) (2003).
115. Moran, J. & Desimone, R. Selective Attention Gates Visual Processing in the Extrastriate Cortex. *Science* **229**, 782–784. ISSN: 0036-8075, 1095-9203. doi:[10.1126/science.4023713](https://doi.org/10.1126/science.4023713) (1985).
116. Nardo, D., Console, P., Reverberi, C. & Macaluso, E. Competition between Visual Events Modulates the Influence of Saliency during Free-Viewing of Naturalistic Videos. *Frontiers in Human Neuroscience* **10**. ISSN: 1662-5161. doi:[10.3389/fnhum.2016.00320](https://doi.org/10.3389/fnhum.2016.00320) (2016).
117. Natale, E., Marzi, C. & Macaluso, E. Right temporal-parietal junction engagement during spatial reorienting does not depend on strategic attention control. *Neuropsychologia* **48**, 1160–1164. ISSN: 00283932. doi:[10.1016/j.neuropsychologia.2009.11.012](https://doi.org/10.1016/j.neuropsychologia.2009.11.012) (2010).
118. Natale, E., Marzi, C. A. & Macaluso, E. fMRI correlates of visuo-spatial reorienting investigated with an attention shifting double-cue paradigm. *Human Brain Mapping* **30**, 2367–2381. ISSN: 10659471, 10970193. doi:[10.1002/hbm.20675](https://doi.org/10.1002/hbm.20675) (2009).
119. Penny, W., Stephan, K., Mechelli, A. & Friston, K. Comparing dynamic causal models. *NeuroImage* **22**, 1157–1172. ISSN: 10538119. doi:[10.1016/j.neuroimage.2004.03.026](https://doi.org/10.1016/j.neuroimage.2004.03.026) (2004).
120. Pessoa, L. Embedding reward signals into perception and cognition. *Frontiers in Neuroscience* **4**. ISSN: 1662453X. doi:[10.3389/fnins.2010.00017](https://doi.org/10.3389/fnins.2010.00017) (2010).
121. Pessoa, L. Multiple influences of reward on perception and attention. *Visual Cognition* **23**, 272–290. ISSN: 1350-6285, 1464-0716. doi:[10.1080/13506285.2014.974729](https://doi.org/10.1080/13506285.2014.974729) (2015).
122. Poldrack, R. A., Mumford, J. A. & Nichols, T. E. *Handbook of functional MRI data analysis* 228 pp. ISBN: 978-0-521-51766-9 (Cambridge Univ. Press, Cambridge, 2011).
123. Poltoratski, S., Ling, S., McCormack, D. & Tong, F. Characterizing the effects of feature salience and top-down attention in the early visual system. *Journal of Neurophysiology* **118**, 564–573. ISSN: 0022-3077, 1522-1598. doi:[10.1152/jn.00924.2016](https://doi.org/10.1152/jn.00924.2016) (2017).
124. Posner, M. I. Orienting of Attention. *Quarterly Journal of Experimental Psychology* **32**, 3–25. ISSN: 0033-555X. doi:[10.1080/00335558008248231](https://doi.org/10.1080/00335558008248231) (1980).

125. Powers, A. R., Kelley, M. & Corlett, P. R. Hallucinations as Top-Down Effects on Perception. *Biological Psychiatry: Cognitive Neuroscience and Neuroimaging* **1**, 393–400. ISSN: 24519022. doi:[10.1016/j.bpsc.2016.04.003](https://doi.org/10.1016/j.bpsc.2016.04.003) (2016).
126. Preciado, D., Munneke, J. & Theeuwes, J. Mixed signals: The effect of conflicting reward- and goal-driven biases on selective attention. *Attention, Perception, & Psychophysics* **79**, 1297–1310. ISSN: 1943-3921, 1943-393X. doi:[10.3758/s13414-017-1322-9](https://doi.org/10.3758/s13414-017-1322-9) (2017).
127. Proulx, M. J. & Egeth, H. E. Biased competition and visual search: the role of luminance and size contrast. *Psychological Research* **72**, 106–113. ISSN: 0340-0727, 1430-2772. doi:[10.1007/s00426-006-0077-z](https://doi.org/10.1007/s00426-006-0077-z) (2007).
128. Ptak, R. The Frontoparietal Attention Network of the Human Brain: Action, Saliency, and a Priority Map of the Environment. *The Neuroscientist* **18**, 502–515. ISSN: 1073-8584, 1089-4098. doi:[10.1177/1073858411409051](https://doi.org/10.1177/1073858411409051) (2012).
129. *Neuroscience* (ed Purves, D.) 4th ed. OCLC: ocn144771764 (Sinauer, Sunderland, Mass, 2008). 857 pp. ISBN: 978-0-87893-697-7.
130. Qin, N., Gu, R., Xue, J., Chen, C. & Zhang, M. Reward-driven attention alters perceived salience. *Journal of Vision* **21**, 7. ISSN: 1534-7362. doi:[10.1167/jov.21.1.7](https://doi.org/10.1167/jov.21.1.7) (2021).
131. Raftopoulos, A. Is perception informationally encapsulated? The issue of the theory-ladenness of perception. *Cognitive Science* **25**, 423–451. ISSN: 03640213. doi:[10.1207/s15516709cog2503_4](https://doi.org/10.1207/s15516709cog2503_4) (2001).
132. Ramachandran, V. S. *Encyclopedia of the human brain* OCLC: 54814129. ISBN: 978-0-08-054803-6 978-1-84972-503-3 (Academic Press, San Diego, Calif., 2002).
133. Rashal, E. *et al.* An EEG study of the combined effects of top-down and bottom-up attentional selection under varying task difficulty. *Psychophysiology*. ISSN: 0048-5772, 1469-8986. doi:[10.1111/psyp.14002](https://doi.org/10.1111/psyp.14002) (2022).
134. Reddy, L., Kanwisher, N. G. & VanRullen, R. Attention and biased competition in multi-voxel object representations. *Proceedings of the National Academy of Sciences of the United States of America* **106**, 21447–21452. ISSN: 1091-6490. doi:[10.1073/pnas.0907330106](https://doi.org/10.1073/pnas.0907330106) (2009).
135. Reynolds, J. H., Chelazzi, L. & Desimone, R. Competitive Mechanisms Subserve Attention in Macaque Areas V2 and V4. *The Journal of Neuroscience* **19**, 1736–1753. ISSN: 0270-6474, 1529-2401. doi:[10.1523/JNEUROSCI.19-05-01736.1999](https://doi.org/10.1523/JNEUROSCI.19-05-01736.1999) (1999).
136. Reynolds, J. H. & Desimone, R. Interacting Roles of Attention and Visual Saliency in V4. *Neuron* **37**, 853–863. ISSN: 08966273. doi:[10.1016/S0896-6273\(03\)00097-7](https://doi.org/10.1016/S0896-6273(03)00097-7) (2003).
137. Richter, D. & de Lange, F. P. Statistical learning attenuates visual activity only for attended stimuli. *eLife* **8**, e47869. ISSN: 2050-084X. doi:[10.7554/eLife.47869](https://doi.org/10.7554/eLife.47869) (2019).
138. Scalf, P. E. & Beck, D. M. Competition in Visual Cortex Impedes Attention to Multiple Items. *Journal of Neuroscience* **30**, 161–169. ISSN: 0270-6474, 1529-2401. doi:[10.1523/JNEUROSCI.4207-09.2010](https://doi.org/10.1523/JNEUROSCI.4207-09.2010) (2010).
139. in. *Advances in Neural Information Processing Systems 19* (eds Schölkopf, B., Platt, J. & Hofmann, T.) (The MIT Press, 2007). ISBN: 978-0-262-25691-9. doi:[10.7551/mitpress/7503.003.0073](https://doi.org/10.7551/mitpress/7503.003.0073).
140. Serences, J. T. Value-Based Modulations in Human Visual Cortex. *Neuron* **60**, 1169–1181. ISSN: 08966273. doi:[10.1016/j.neuron.2008.10.051](https://doi.org/10.1016/j.neuron.2008.10.051) (2008).
141. Seymour, K., Clifford, C. W., Logothetis, N. K. & Bartels, A. The Coding of Color, Motion, and Their Conjunction in the Human Visual Cortex. *Current Biology* **19**, 177–183. ISSN: 09609822. doi:[10.1016/j.cub.2008.12.050](https://doi.org/10.1016/j.cub.2008.12.050) (2009).

142. Shapcott, K. A. *et al.* Reward-Related Suppression of Neural Activity in Macaque Visual Area V4. *Cerebral Cortex* **30**, 4871–4881. ISSN: 1047-3211, 1460-2199. doi:[10.1093/cercor/bhaa079](https://doi.org/10.1093/cercor/bhaa079) (2020).
143. Silver, M. A. & Kastner, S. Topographic maps in human frontal and parietal cortex. *Trends in Cognitive Sciences* **13**, 488–495. ISSN: 13646613. doi:[10.1016/j.tics.2009.08.005](https://doi.org/10.1016/j.tics.2009.08.005) (2009).
144. Simons, D. J. & Chabris, C. F. Gorillas in Our Midst: Sustained Inattentive Blindness for Dynamic Events. *Perception* **28**, 1059–1074. ISSN: 0301-0066, 1468-4233. doi:[10.1068/p281059](https://doi.org/10.1068/p281059) (1999).
145. Smith, A. T., Singh, K. D. & Greenlee, M. W. Attentional suppression of activity in the human visual cortex: *NeuroReport* **11**, 271–278. ISSN: 0959-4965. doi:[10.1097/00001756-200002070-00010](https://doi.org/10.1097/00001756-200002070-00010) (2000).
146. Somers, D. C., Dale, A. M., Seiffert, A. E. & Tootell, R. B. H. Functional MRI reveals spatially specific attentional modulation in human primary visual cortex. *Proceedings of the National Academy of Sciences* **96**, 1663–1668. ISSN: 0027-8424, 1091-6490. doi:[10.1073/pnas.96.4.1663](https://doi.org/10.1073/pnas.96.4.1663) (1999).
147. Sprague, T. C., Itthipuripat, S., Vo, V. A. & Serences, J. T. Dissociable signatures of visual salience and behavioral relevance across attentional priority maps in human cortex. *Journal of Neurophysiology* **119**, 2153–2165. ISSN: 1522-1598. doi:[10.1152/jn.00059.2018](https://doi.org/10.1152/jn.00059.2018) (2018).
148. Stanisor, L., van der Togt, C., Pennartz, C. M. A. & Roelfsema, P. R. A unified selection signal for attention and reward in primary visual cortex. *Proceedings of the National Academy of Sciences* **110**, 9136–9141. ISSN: 0027-8424, 1091-6490. doi:[10.1073/pnas.1300117110](https://doi.org/10.1073/pnas.1300117110) (2013).
149. Stephan, K. E. *et al.* Dynamic causal models of neural system dynamics: current state and future extensions. *Journal of Biosciences* **32**, 129–144. ISSN: 0250-5991, 0973-7138. doi:[10.1007/s12038-007-0012-5](https://doi.org/10.1007/s12038-007-0012-5) (2007).
150. Stephan, K. *et al.* Ten simple rules for dynamic causal modeling. *NeuroImage* **49**, 3099–3109. ISSN: 10538119. doi:[10.1016/j.neuroimage.2009.11.015](https://doi.org/10.1016/j.neuroimage.2009.11.015) (2010).
151. Suzuki, M. & Gottlieb, J. Distinct neural mechanisms of distractor suppression in the frontal and parietal lobe. *Nature Neuroscience* **16**, 98–104. ISSN: 1097-6256, 1546-1726. doi:[10.1038/nn.3282](https://doi.org/10.1038/nn.3282) (2013).
152. Swisher, J. D., Halko, M. A., Merabet, L. B., McMains, S. A. & Somers, D. C. Visual Topography of Human Intraparietal Sulcus. *Journal of Neuroscience* **27**, 5326–5337. ISSN: 0270-6474, 1529-2401. doi:[10.1523/JNEUROSCI.0991-07.2007](https://doi.org/10.1523/JNEUROSCI.0991-07.2007) (2007).
153. Tehovnik, E. J., Sommer, M. A., Chou, I.-H., Slocum, W. M. & Schiller, P. H. Eye fields in the frontal lobes of primates. *Brain Research Reviews* **32**, 413–448. ISSN: 01650173. doi:[10.1016/S0165-0173\(99\)00092-2](https://doi.org/10.1016/S0165-0173(99)00092-2) (2000).
154. Theeuwes, J. Stimulus-driven capture and attentional set: selective search for color and visual abrupt onsets. *Journal of Experimental Psychology. Human Perception and Performance* **20**, 799–806. ISSN: 0096-1523. doi:[10.1037//0096-1523.20.4.799](https://doi.org/10.1037//0096-1523.20.4.799) (1994).
155. Theeuwes, J. Top-down and bottom-up control of visual selection. *Acta Psychologica* **135**, 77–99. ISSN: 00016918. doi:[10.1016/j.actpsy.2010.02.006](https://doi.org/10.1016/j.actpsy.2010.02.006) (2010).
156. Theeuwes, J. Visual Selection: Usually Fast and Automatic; Seldom Slow and Volitional. *Journal of Cognition* **1**, 29. ISSN: 2514-4820. doi:[10.5334/joc.13](https://doi.org/10.5334/joc.13) (2018).
157. Thomas, F., Lefevre, T. & Raymond, M. *Biologie évolutive* 2e éd. ISBN: 978-2-8073-0296-9 (De Boeck supérieur IRD, Institut de recherche pour le développement CNRS, Louvain-la-Neuve (Belgique), 2016).

158. Thompson, K. G. & Bichot, N. P. in *Progress in Brain Research* 249–262 (Elsevier, 2005). ISBN: 978-0-444-51663-3. doi:[10.1016/S0079-6123\(04\)47019-8](https://doi.org/10.1016/S0079-6123(04)47019-8).
159. Thomsen, T., Specht, K., Ersland, L. & Hugdahl, K. Processing of conflicting cues in an attention-shift paradigm studied with fMRI. *Neuroscience Letters* **380**, 138–142. ISSN: 03043940. doi:[10.1016/j.neulet.2005.01.026](https://doi.org/10.1016/j.neulet.2005.01.026) (2005).
160. Todd, R. M. & Manaligod, M. G. Implicit guidance of attention: The priority state space framework. *Cortex* **102**, 121–138. ISSN: 00109452. doi:[10.1016/j.cortex.2017.08.001](https://doi.org/10.1016/j.cortex.2017.08.001) (2018).
161. Tootell, R. B. *et al.* The Retinotopy of Visual Spatial Attention. *Neuron* **21**, 1409–1422. ISSN: 08966273. doi:[10.1016/S0896-6273\(00\)80659-5](https://doi.org/10.1016/S0896-6273(00)80659-5) (1998).
162. Turova, T. & Rolls, E. T. Analysis of Biased Competition and Cooperation for Attention in the Cerebral Cortex. *Frontiers in Computational Neuroscience* **13**, 51. ISSN: 1662-5188. doi:[10.3389/fncom.2019.00051](https://doi.org/10.3389/fncom.2019.00051) (2019).
163. Tzourio-Mazoyer, N. *et al.* Automated Anatomical Labeling of Activations in SPM Using a Macroscopic Anatomical Parcellation of the MNI MRI Single-Subject Brain. *NeuroImage* **15**, 273–289. ISSN: 10538119. doi:[10.1006/nimg.2001.0978](https://doi.org/10.1006/nimg.2001.0978) (2002).
164. Veale, R., Hafed, Z. M. & Yoshida, M. How is visual salience computed in the brain? Insights from behaviour, neurobiology and modelling. *Philosophical Transactions of the Royal Society B: Biological Sciences* **372**, 20160113. ISSN: 0962-8436, 1471-2970. doi:[10.1098/rstb.2016.0113](https://doi.org/10.1098/rstb.2016.0113) (2017).
165. Vossel, S., Weidner, R., Driver, J., Friston, K. J. & Fink, G. R. Deconstructing the Architecture of Dorsal and Ventral Attention Systems with Dynamic Causal Modeling. *Journal of Neuroscience* **32**, 10637–10648. ISSN: 0270-6474, 1529-2401. doi:[10.1523/JNEUROSCI.0414-12.2012](https://doi.org/10.1523/JNEUROSCI.0414-12.2012) (2012).
166. Vossel, S., Geng, J. J. & Fink, G. R. Dorsal and Ventral Attention Systems: Distinct Neural Circuits but Collaborative Roles. *The Neuroscientist* **20**, 150–159. ISSN: 1073-8584, 1089-4098. doi:[10.1177/1073858413494269](https://doi.org/10.1177/1073858413494269) (2014).
167. Vossel, S., Mathys, C., Stephan, K. E. & Friston, K. J. Cortical Coupling Reflects Bayesian Belief Updating in the Deployment of Spatial Attention. *The Journal of Neuroscience* **35**, 11532–11542. ISSN: 0270-6474, 1529-2401. doi:[10.1523/JNEUROSCI.1382-15.2015](https://doi.org/10.1523/JNEUROSCI.1382-15.2015) (2015).
168. Vuilleumier, P. How brains beware: neural mechanisms of emotional attention. *Trends in Cognitive Sciences* **9**, 585–594. ISSN: 13646613. doi:[10.1016/j.tics.2005.10.011](https://doi.org/10.1016/j.tics.2005.10.011) (2005).
169. Wolfe, J. M., Butcher, S. J., Lee, C. & Hyle, M. Changing your mind: On the contributions of top-down and bottom-up guidance in visual search for feature singletons. *Journal of Experimental Psychology: Human Perception and Performance* **29**, 483–502. ISSN: 1939-1277, 0096-1523. doi:[10.1037/0096-1523.29.2.483](https://doi.org/10.1037/0096-1523.29.2.483) (2003).
170. Won, B.-Y., Forloines, M., Zhou, Z. & Geng, J. J. Changes in visual cortical processing attenuate singleton distraction during visual search. *Cortex* **132**, 309–321. ISSN: 00109452. doi:[10.1016/j.cortex.2020.08.025](https://doi.org/10.1016/j.cortex.2020.08.025) (2020).
171. Yantis, S. How visual salience wins the battle for awareness. *Nature Neuroscience* **8**, 975–977. ISSN: 1097-6256, 1546-1726. doi:[10.1038/nm0805-975](https://doi.org/10.1038/nm0805-975) (2005).
172. Yoshida, M. *et al.* Residual Attention Guidance in Blindsight Monkeys Watching Complex Natural Scenes. *Current Biology* **22**, 1429–1434. ISSN: 09609822. doi:[10.1016/j.cub.2012.05.046](https://doi.org/10.1016/j.cub.2012.05.046) (2012).
173. Zeidman, P. *et al.* A guide to group effective connectivity analysis, part 1: First level analysis with DCM for fMRI. *NeuroImage* **200**, 174–190. ISSN: 10538119. doi:[10.1016/j.neuroimage.2019.06.031](https://doi.org/10.1016/j.neuroimage.2019.06.031) (2019).

174. Zelinsky, G. J. & Bisley, J. W. The what, where, and why of priority maps and their interactions with visual working memory: The what, where, and why of priority maps. *Annals of the New York Academy of Sciences* **1339**, 154–164. ISSN: 00778923. doi:[10.1111/nyas.12606](https://doi.org/10.1111/nyas.12606) (2015).
175. Zhang, B. *et al.* *Statistical learning of frequent distractor locations in visual search involves regional signal suppression in early visual cortex* preprint (Neuroscience, 2021). doi:[10.1101/2021.04.16.440127](https://doi.org/10.1101/2021.04.16.440127).
176. Zivony, A., Shanny, S. & Lamy, D. Perceptual Processing is Not Spared During the Attentional Blink. *Journal of Cognition* **1**, 18. ISSN: 2514-4820. doi:[10.5334/joc.20](https://doi.org/10.5334/joc.20) (2018).