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Spatio-temporal dynamics of attentional cycles : a computational and neuroimaging approach

Garance Merholz

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Thèse dirigée par **Laura DUGUÉ**

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Abstract

Perception and attention are fundamental cognitive functions for understanding and interacting with our environment. Brain oscillations of various temporal frequencies correlate with these psychological functions. Particularly, low-frequency rhythms termed theta (4-8 Hz) and alpha (8-14 Hz) seem to play an important role in perception and attention. The general relation between oscillatory frequencies and associated cognitive processes is beginning to be understood, but much is left to speculation. This thesis aims to characterize the role of brain oscillations in perception and attention by focusing on both their temporal and spatial dynamics. The first axis of this work aims to explain the large discrepancies in temporal frequency observed in the literature on attention. We propose that it may be due to differences in attentional demands, resulting from heterogeneity in tasks performed. Using visual search tasks combined with electro-encephalography, we replicate previous findings of pre-stimulus cortical phase and post-stimulus phase reset influencing performance. Critically, we show that these phase effects occur in rising frequency and latency with task complexity. These novel findings confirm that the fine temporal tuning of neural oscillations directly relates to cognitive functioning and behavior. The second axis focuses on the spatio-temporal dynamics of brain oscillations involved in cognition. The spatial properties of cortical oscillatory waves of activity have only recently begun to form a topic of study in neuroscientific research. Here, we review the traveling property of oscillatory waves propagating across the brain and model such oscillatory traveling waves in the human visual cortex. This project is the first stage towards the creation of a computational tool for measuring traveling waves in healthy humans, using non-invasive techniques of electro- and magneto-encephalography. Such a tool will enable model-based neuroimaging of neural oscillatory activity, circumventing the issues of the classic inverse modeling framework. In conclusion, the first axis of this thesis provides additional evidence that brain oscillations support attentional sampling and the second works to provide a new tool to investigate the understudied spatial dimension of these oscillations.

Résumé en français

La perception et l'attention sont des fonctions cognitives fondamentales et nécessaires à l'appréhension du monde extérieur. Certaines oscillations cérébrales enregistrées à la surface du crâne corrélerent avec ces fonctions psychologiques, en particulier les rythmes à basse fréquence thêta (4-8 Hz) et alpha (8-14 Hz). Les neurosciences cognitives ont entamé la question de la relation entre les fréquences oscillatoires et les processus cognitifs qui leur sont associés, mais de nombreuses questions subsistent. Cette thèse vise à caractériser le rôle des oscillations cérébrales dans la perception et l'attention en s'intéressant à leurs dynamiques temporelles et spatiales.

Dans un premier temps, nous couvrons les aspects théoriques de la littérature existante sur la relation entre la perception et l'attention, ainsi que ses fondements neuronaux. Nous montrons que l'attention est une fonction cognitive essentielle qui module les mesures comportementales et neurales lors de tâches perceptives. Cette modulation attentionnelle a été démontrée à l'aide de plusieurs outils tels que la psychophysique, les enregistrements intracorticaux et la neuroimagerie non invasive. Chez les primates, l'attention module les neurones visuels et aurait pour origine un réseau attentionnel dédié. Des méthodes d'enregistrements cérébraux à échelle macroscopique ont permis de décrire le réseau attentionnel dans le cerveau humain. Cette caractérisation repose notamment sur la mesure d'oscillations neurales par électroencéphalographie (EEG) et magnétoencéphalographie (MEG). Nous montrons que la modélisation cognitive et computationnelle permet une meilleure compréhension des processus cognitifs, notamment ceux impliqués dans le contrôle attentionnel. Nous présentons les principales théories et modèles computationnels rendant compte des données neurophysiologiques existantes. Ces modèles guident notre conception des mécanismes neuronaux de la perception et de l'attention. Ils produisent d'importantes prédictions pour des expérimentations futures. Enfin, la relation entre les oscillations corticales et la cognition, en particulier la perception et l'attention, est introduite. Une première hypothèse de leur organisation spatiale, l'hypothèse *spatiale statique*, est présentée. Ces modèles postulent une synchronisation de signaux statiques, chacun localisé dans sa propre aire corticale. Cependant, les oscillations présentant une synchronicité sont suffisamment proéminents pour atteindre les électrodes EEG à la surface du crâne, ce qui implique que l'activité des neurones est importante. De plus, ces neurones sont fortement connectés les uns aux autres, et leur activité électrique se répand dans l'espace : c'est justement grâce à cette propagation spatiale que le signal peut atteindre les électrodes placées à l'extérieur du crâne. L'activité électrique se propage donc depuis la source vers l'extérieur, donc il doit nécessairement y avoir une propagation à la surface du cortex. Il a été proposé que cette propagation a une fonction pour la cognition et le comportement : des hypothèses alternatives, qui n'excluent pas nécessairement l'hypothèse *spatiale statique* mais peuvent la compléter, suggèrent que la propagation de l'activité corticale est pertinente et remplit une fonction dans l'organisation spatiale des signaux cérébraux.

L'objectif de cette thèse est de fournir une description détaillée du rôle des oscillations cérébrales dans la perception et l'attention. Nous montrons que l'attention doit être sélective et flexible. Elle optimise la perception dans la tâche actuelle, mais elle doit aussi s'adapter à de nouveaux contextes et dépendre fortement de l'environnement, souvent changeant. Ainsi, l'attention doit pouvoir basculer efficacement et rapidement entre les tâches et les stimuli. Des études passées montrent que les processus attentionnels dans le système neuronal humain attestent d'une grande flexibilité et d'une adaptabilité à de nombreuses tâches.

Dans le chapitre II, nous nous concentrons sur les propriétés temporelles des oscillations neuronales impliquées dans la perception visuelle et l'attention. Nous présentons une nouvelle étude élargissant les connaissances déjà existantes sur les effets de fréquence et de phase

oscillatoire sur les performances attentionnelles. L'hypothèse d'un échantillonnage cognitif régulier propose que l'attention et la perception subissent des cycles réguliers de baisse et de hausse de traitement. Cette hypothèse a reçu le soutien de nombreuses études, mais les fréquences rapportées sont hétérogènes. Nous émettons la nouvelle hypothèse que le cerveau peut adapter sa synchronisation temporelle pour faire face à différents niveaux de difficulté de la tâche, et plus particulièrement à son exigence au niveau attentionnel. Ce premier axe expérimental vise donc à expliquer les grands écarts de fréquence temporelle observés dans la littérature sur l'échantillonnage attentionnel. Nous proposons que ces écarts soient dûs à des différences de demandes attentionnelles, résultant de l'hétérogénéité des tâches effectuées. De plus, la plupart des études présentées dans la littérature existante utilise des manipulations simples, généralement binaires, de l'attention ("avec" ou "sans" attention, qu'elle soit spatiale ou basée sur les objets). Il est primordial de prendre en compte des effets attentionnels plus précis. En modifiant les paramètres d'une recherche visuelle, nous pouvons décrire des différences subtiles dans la capture attentionnelle, la sélection et l'échantillonnage temporellement régulier. Grâce à de puissants outils de calcul, il est possible de décomposer la phase des oscillations neuronales et ainsi évaluer les mécanismes corticaux associés. Ces outils offrent la possibilité d'explorer les mécanismes neuraux donnant lieu aux différences comportementales entre des configurations de recherche visuelle. Nous introduisons un nouveau paradigme pour tester la sélectivité des processus attentionnels dans des contextes similaires, mais non identiques. Nous testons la capacité de l'attention et la perception à s'adapter sur une courte échelle de temps. En utilisant des tâches de recherche visuelle à niveau variable de difficulté (discriminabilité élevée, moyenne ou basse de la cible par rapport au distracteur, et nombre variable d'items) combinées à l'EEG, nous reproduisons des effets rapportés précédemment d'une influence de la phase (avant l'apparition des stimuli) et de la cohérence de phase (après apparition des items) sur la performance des participants. Nous montrons que ces effets de phase se produisent dans une fréquence et à une latence croissantes suivant la complexité de la tâche, et qu'ils ne peuvent pas s'expliquer par une différence de taux de succès, ni par une différence de temps de présentation des stimuli, à travers les différentes conditions. En revanche, la fréquence des oscillations présentant une opposition de phase (pré-stimulus) ne corrèle pas avec celle présentant une cohérence de phase après l'apparition des stimuli. Ce constat suggère que les effets d'opposition de phase sont dissociés des effets de phase dans les oscillations évoquées par le stimulus. Dans l'ensemble, ces nouvelles découvertes suggèrent qu'un ajustement temporel précis des oscillations neuronales est directement lié au fonctionnement cognitif et au comportement. De plus, nos résultats sur la fréquence croissant avec la difficulté semblent s'opposer aux résultats passés, qui suggèrent que les processus attentionnels (sous-tendant des tâches plus complexes) donnent lieu à des oscillations cérébrales à basse fréquence, tandis que les tâches perceptuelles et donc plus simples du point de vue cognitif seraient associées à de hautes fréquences. Nous proposons que nos résultats, en opposition apparente à cette vision classique, traduisent une subtilité des mécanismes de l'attention et reflètent les cycles oscillatoires impliqués dans la gestion des demandes attentionnelles pendant les tâches cognitives.

Cette étude a été postée sous forme de pré-rapport sur la plateforme bioRxiv et soumise à la revue internationale à comité de lecture *Scientific Reports* pour publication. Le rapport est inclus dans la thèse à la page 79. Il est identifié sous la référence :

Merholz, G., Grabot, L., VanRullen, R., & Dugué, L. (2021). *Periodic Attention Operates Faster During More Complex Visual Search*. Preprint; under review at *Scientific Reports*. bioRxiv DOI: 10.1101/2021.09.22.460906

Les propriétés spatiales des oscillations neuronales peuvent également jouer un rôle fondamental dans la cognition, mais elles n'ont que récemment commencé à faire l'objet de recherches

neuroscientifiques. Certaines études rapportent la présence d'ondes cérébrales ayant une dynamique spatiale à travers le cortex. La phase, la fréquence et l'amplitude de ces ondes affecteraient les processus perceptifs et attentionnels. Ce domaine requiert plus de preuves de leur impact comportemental. Le second axe de la thèse porte donc sur la dynamique spatio-temporelle des oscillations cérébrales impliquées dans la cognition. Dans le chapitre III, nous explorons comment une structuration spatiale flexible peut aider à transmettre de l'information et la traiter efficacement. Nous couvrons les avancées récentes dans la compréhension des propriétés spatiales des ondes corticales et montrons la nécessité d'une approche de neuroimagerie basée sur des modèles théoriques. Nous proposons donc une nouvelle méthode de neuroimagerie ayant pour but d'évaluer la propagation des ondes corticales oscillatoires. Nous nous basons sur les propriétés rapportées précédemment des ondes se déplaçant à travers le cortex et nous modélisons des ondes oscillatoires dans le cortex visuel humain. Ce projet constitue la première étape dans la création d'un outil computationnel destiné à mesurer les ondes propagatrices chez l'humain sain, en utilisant des techniques non invasives d'EEG et MEG. Un tel outil permettra une neuroimagerie basée sur un modèle de l'activité oscillatoire neuronale, contournant ainsi les problèmes de la modélisation inverse classique. Nous exposons nos méthodes dans la création de stimuli destinés à éliciter des oscillations se propageant à la surface du cortex avec les caractéristiques (phase, amplitude, fréquence...) attendues d'après les résultats existants dans la littérature. Ces méthodes se basent sur la correspondance entre les relations spatiales dans le champ visuel et le cortex visuel primaire, et prennent en compte les distortions dues à la magnification corticale. Enfin, nous présentons un modèle computationnel permettant d'expliquer l'apparition de ces ondes à partir du couplage partiel de sous-populations oscillant spontanément à la surface du cortex.

Le travail expérimental présenté dans ce chapitre fait partie d'un projet collaboratif visant à l'implémentation d'un modèle biologiquement plausible de la propagation des ondes corticales. Ce projet est en cours, mais il a donné lieu à la présentation d'un premier poster scientifique référencé comme suit :

Grabot, L., Merholz, G., Winawer, J., Heeger, D., & Dugué, L. (2021). Computational Modeling of MEG-EEG Oscillatory Traveling Waves In Human. *Groupe de Recherche (GDR) Vision Annual Conference*.

Pour conclure, le premier axe de cette thèse fournit des preuves supplémentaires que les oscillations cérébrales sous-tendent l'échantillonnage attentionnel, et le second décrit la création d'un nouvel outil pour étudier la dimension spatiale sous-étudiée de ces oscillations. Dans cette thèse, nous avons montré que les propriétés temporelles et spatiales précises des oscillations enregistrées à la surface du scalp sont à la fois des marqueurs cruciaux de l'activité neuronale et, à plus grande échelle, de la cognition elle-même. Nous avons exploré la dynamique spatio-temporelle des oscillations neurales, d'abord par la manipulation comportementale des tâches de recherche visuelle avec enregistrement EEG simultané, et ensuite par la modélisation computationnelle du cortex visuel. Nos contributions ne tranchent pas sur la question du rôle des oscillations dans la cognition et le comportement, mais elles soutiennent un lien étroit entre eux. De nombreuses autres expériences sont nécessaires pour étoffer les questions demeurant sans réponse, ajoutées à celles nouvellement soulevées par notre travail. Le rôle des oscillations neuronales dans le comportement humain reste un casse-tête en grande partie non résolu, mais nous espérons avoir utilement arrangé quelques pièces du puzzle.

Publications and Scientific Communication

International peer-reviewed journal submission

Merholz, G., Grabot, L., VanRullen, R., & Dugué, L. (2021). *Periodic Attention Operates Faster During More Complex Visual Search*. Preprint; under review at *Scientific Reports*. bioRxiv DOI: 10.1101/2021.09.22.460906

Communication in national and international conferences

Grabot, L., Merholz, G., Winawer, J., Heeger, D., & Dugué, L. (2021). Computational Modeling of MEG-EEG Oscillatory Traveling Waves In Human. *Groupe de Recherche (GDR) Vision Annual Conference* (poster)

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Merholz, G., VanRullen, R., & Dugué, L. (2018). Oscillations Modulate Attentional Search Performance Periodically. *Groupe de Recherche (GDR) Vision Annual Conference* (poster)

Invited talks

Institut du Cerveau (ICM) - Presentation of the Temporal Dynamics project at the PICNIC lab

Context and collaborations

The work presented in this thesis has of course not been performed by the candidate alone. Many researchers have contributed. Laura Dugué and Rufin VanRullen⁽¹⁾ jointly designed the study presented in Chapter II, and Laura Dugué performed the data collection for this project. She and Laetitia Grabot⁽²⁾ assisted Garance Merholz in analyzing the resulting data. The production of the report presenting this study was a joint effort between Garance Merholz, Laetitia Grabot, Rufin VanRullen, and Laura Dugué. The connectivity analysis presented in the complementary results was performed by Clélia Cornet⁽²⁾. The designs of the source model, visual wave inducer, and coupled oscillator model presented in Chapter III are the result of an active collaboration between Laetitia Grabot, Garance Merholz, Jonathan Winawer⁽³⁾, David Heeger⁽³⁾, and Laura Dugué, with help from Chrysa Papadaniil⁽⁴⁾. The wave inducer design also received help from Maximilien Chaumon⁽⁵⁾. Encephalographic data were collected by Laetitia Grabot and Damien Boyer⁽²⁾ using the MEG and EEG at the CENIR, Institut du Cerveau (ICM), with Christophe Gitton⁽⁵⁾ and Laurent Hugueville⁽⁵⁾'s precious help.

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Foreword

Cognitive neuroscience is a discipline right at the frontier between psychology and biology. As cognitive neuroscientists, we strive to ally forces between these two domains, using methods from both to describe the mind in a complete and logically sound manner. One thing seems clear from cognitive research so far: the brain's activity relates to the mind in countless ways. This close link makes the brain the best candidate for the support of the mind, which includes explicit thought and all of our unconscious, background psychological activity. Thus, cognitive neuroscience is broadly infused with physicalism, the idea that mind and matter are not separate entities but rather that the physical support (the brain) gives rise exclusively to the psychological reality (the mind). That is not to say that the mind can be reduced to its material substrates. Cognition is a vastly complex world in itself, and cognitive neuroscience is equally interested in defining its psychological mechanisms and extracting how the brain might realize them.

The mechanisms that give rise to how, what, and why we think are as vast and mysterious as the universe. To tackle the relationship between brain and mind, it seems necessary to decompose it into elemental parts. The field has broadly categorized mental processes into *cognitive functions*, including perception and attention. Perception is what gives the mind access to the outside world. As we will see, perception relies heavily on attention to parse through the overabundance of information entering our sensory portals at any given time. Studying perception and attention seems like a good place to begin understanding how the mind works and how the brain can give rise to these functions.

Thanks to the technology currently at our disposal, we know that one notable way the brain organizes itself is through temporal synchrony, which significantly contributes to the mechanisms of perception and attention. The present thesis focuses on the links between neural oscillations and cognition, a topic that has already incurred substantial research. Our goal is not to start from scratch but to provide new pieces to this expansive puzzle. This thesis aims to review the current state of this growing field and present our novel contributions.

I
GENERAL INTRODUCTION

1 Attention as a cognitive process to control perception

It has long since been shown that perception is not a passive activity. Intuitively, it is easy to think that the information coming in from the external, physical world is instantly "imported" as-is into the perceptual system and that through this process, we have direct and unfaltering access to our environment. Our daily experience when interacting with the world is of direct and unaltered contact. However, our subjective experience does not correspond to how the brain truly functions. The brain and the perceptual processes within it perform an incredible amount of modulations on the incoming information (Edelman, 1989; Marr, 1982). One rather basic example is attention.

1.1 What is attention?

In everyday language, attention is usually conceived as focus, i.e., the ability to concentrate on something. It implies prioritizing one specific element and ignoring everything else. This standard definition of attention is the type that interested early researchers. Hermann von Helmholtz laid the foundation for the operationalization of psychological research by advocating for a systematic parcellation of cognitive functions (see, e.g., von Helmholtz, 1885). He understood that attention is too complex to study in one block. His student, Wilhelm Wundt, is now considered one of the founders of experimental psychology. The main difference in approach between the two researchers is that Wundt considered the mind as a separate entity from the body, whereas von Helmholtz was interested in the relation between them, putting a significant emphasis on materialism (Bowler & Morus, 2005). William James gave a broad definition of attention in his famous quote:

"Everyone knows what attention is. It is the taking possession by the mind, in clear and vivid form, of one out of what seem several simultaneously possible objects or trains of thought. Focalization, concentration, of consciousness are of its essence. It implies withdrawal from some things in order to deal effectively with others, and is a condition which has a real opposite in the confused, dazed, scatterbrained state." (James, 1890, p. 403)

Since then, attention has been the topic of considerable research. Following in von Helmholtz's footsteps, more specific definitions and categorizations of attention as a psychological and neural mechanism have arisen. There is still much debate around what attention essentially is, but certain aspects of it are indubitable.

In psychology and neuroscience, attention is the cognitive function that allows an individual (human or other) to **select** and **facilitate** the processing of some particular subpart of the enormous ensemble of sensory information streaming into the senses in a constant flow (Carrasco, 2011; Rensink, 2000). Attention allows us to make sense of the world by segmenting the information at hand and selectively prioritizing the elements of interest to the individual, in that specific context, and at that given time point. It seems selective in that it converges on only a minimal subset at a time. It also needs to be highly flexible to allow tracking of multiple items at once and remaining alert to unanticipated relevant stimuli. For example, the "cocktail party effect" shows that one can be absorbed into a conversation and ignore all other speech around them in a crowded room, but still react if their first name is uttered by someone other than their discussion partner (Moray, 1959).

Thus, if perception can be loosely defined as the body of mechanisms tasked to handle the early intake of sensory information, attention is the step just following it, without which we would not be able to make sense of the world. Attention and perception are considered separate cognitive functions because perception effects are modality-specific (e.g., it does not affect vision, audition, and olfaction in the same ways), whereas attention may affect all sensory modalities in equivalent ways. From this point of view, attention was divided into categories or sub-types, which make it much easier to study using the scientific method: overt vs. covert, i.e., accompanied by eye movements to indicate the focus of attention, or not; exogenous vs. endogenous, i.e., attention that is involuntarily directed towards an object that "grabs" our focus despite our will, or the voluntary control of one's attention towards something; spatial vs. object- or feature-based. New types of attention have recently been defined (e.g., temporal attention), but we will not discuss these further. We will review how classic attentional types are defined and tested in the cognitive neuroscience literature.

1.2 Behavioral evaluation of attention

It is impossible to understand the mind without obtaining some concrete data about our behavior. Behavioral measures are an essential tool to study how the external world is reflected in the psyche and how psychological processes make it possible to interact with our environment.

1.2.1 Psychophysics

One of the main interests of psychophysics has been to measure thresholds, and more specifically, thresholds of sensation. For example, one of the original questions of psychophysics was, "What is the minimum intensity of light that a person can detect?" Thus, psychophysicists set about to measure the relationship between objective, experimentally controlled stimulation from the physical world and subjective, reported sensation from the internal, sensing mind. From the first type of question, a second one naturally followed: "What is the minimum difference in intensity between two light sources that will lead an observer to perceive them as different?" Ernst Weber was the first to show that this minimum disparity, termed "just noticeable difference" (JND), is a constant fraction of the stimulus' intensity (Gescheider, 2013). Many others followed as psychophysics became of increasing interest as a scientifically valid tool to measure sensation and perception. Gustav Fechner coined the term for this discipline in the first book describing its methods (Fechner, 1860). Whereas Weber had focused on the senses of touch and vision, Fechner extended Weber's work to encompass other senses and systematized the study of the relationship between matter and mind.

An essential contribution of psychophysics is the staircase design, allowing experimenters to approximate the participant's threshold with high precision. In a staircase procedure, the stimulation intensity is varied step by step. At the same time, the participant is continuously probed about their sensation, e.g., by reporting whether they sense the stimulation or not. Typically, the initially distant stimulation steps are gradually reduced as the intensity circles closer and closer to the participant's threshold until small changes in stimulus intensity yield opposite reports, i.e., a precise estimate of the participant's threshold is found.

Beyond threshold measures and providing essential but relatively simple information about the relationship between stimuli intensity and sensation, the field of psychophysics was developed and expanded to test precise behavioral mechanisms (Caputo & Guerra, 1998) and even to test the predictions of neuronal models (Bahcall & Kowler, 1999; Cutzu & Tsotsos, 2003), as we will see in detail in Sections 1.3 and 2.3.2.

1.2.2 Signal Detection Theory

If the reader has ever looked up at the night sky looking for shooting stars, they may remember experiencing a visual "false alarm:" a glimmer out of the corner of their eye that could have been what they were searching for, but which they dismissed as another, flickering light or an insect flying by, or even a figment of their imagination. Indeed, neurons along the visual pathway often fire at random even when nothing is physically present in the visual field, leading us to experience internally produced glimmers. One problem is that certain external stimuli, such as a faint shooting star, are hardly discriminable from random external flickers or internal neuronal noise, precisely because those same neurons that fire in response to a faint stimulus also randomly fire and produce the minor hallucinations (Wilmshurst, 1990). So how do we decide whether a faint perception is what we seek or noise? Signal Detection Theory (SDT, McNicol, 2005) posits that the neuronal responses to informative stimuli (shooting stars) have some overlap with those for distracting noise (random external or internal patterns; see Figure I.1.1). The amount of overlap between these responses determines the observer's sensitivity to the informative signal. In the case of high overlap (e.g., very faint shooting stars and imaginary glimmers), their sensitivity will be very low. In those situations especially, the observer must set a limit between the two types of response: this limit is called the "criterion." Any response falling to one side of the criterion will be interpreted as an informative stimulus, even if it comes from a distracting pattern in reality, and any response falling to the other side will be dismissed as noise. According to SDT, rejecting a glimmer in the night sky is due to its neural response falling to the "noise" side of the set criterion. It may be impossible to verify whether one has correctly rejected a distracting noise pattern or missed an actual signal in these everyday situations. However, we may recreate such ambiguous situations in the laboratory and know whether the observer was right or wrong in their perceptual decision. SDT has established a vocabulary for the four possibilities: a "hit" occurs when the observer correctly categorizes the pattern as an informative signal; a "miss" corresponds to the stimulation being identical but incorrectly categorized as noise; a "false alarm" means that the participant reported seeing an informative stimulus, whereas they did not; and of course a "correct rejection" is a correct categorization of noise as such. The rate of occurrence of these four outcomes is used to calculate d -prime, which quantifies sensitivity and thus informs us about the overlap between signal and

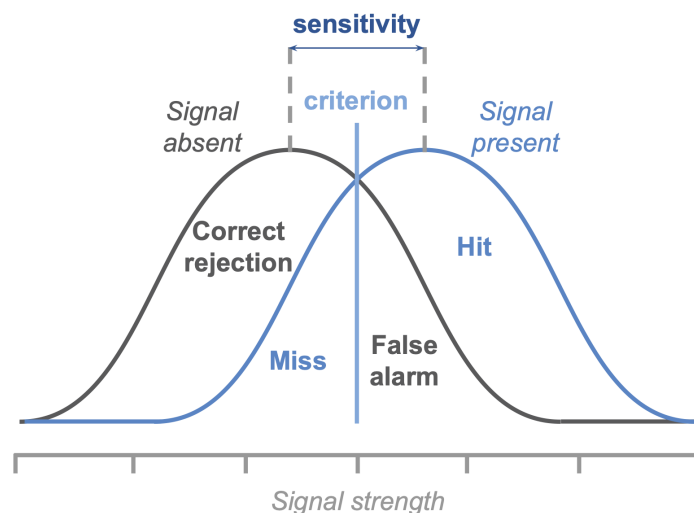


Figure I.1.1: Illustration of signal detection theory. The gray distribution (left) corresponds to signal strength when the signal is absent, i.e., due to noise. The blue distribution (right) represents signal strength as a response to the signal, e.g., a shooting star.

noise responses, and the criterion, which may vary over time. SDT is an important addition to traditional psychophysical methods because it allows experimenters to make a distinction between purely sensory effects and potential perceptual biases (Green, Swets, et al., 1966).

Recent research has applied the original methods of psychophysics and signal detection theory (SDT) to attention and its sub-categories in an effort to develop rigorous tests of attentional effects on perception (Braun, 1998; Carrasco, 2006; Cavanagh & Alvarez, 2005; Lu & Doshier, 2008; Sperling & Melchner, 1978; Verghese, 2001). With these advanced methods, a more strict characterization of attention as a controller of perception arose (Reynolds & Heeger, 2009).

1.2.3 Behavioral evidence that attention affects perception

1.2.3.1 Early findings

Early research used double-task paradigms to test attention. In a dichotic listening task (Cherry, 1953; Moray, 1959), participants wear headphones. They hear a first stream of speech in one ear, which they repeat in real-time, so experimenters may directly assess whether they are paying attention to it and how well. Simultaneously, another stream of speech flows to the opposite ear. This task is difficult, so participants must actively ignore the second ear. Dichotic listening tasks allowed early experimenters to measure which properties of speech are processed without effort: participants could report them even in the ignored speech. The spoken language, whether the speaker was male or female, and whether the listener's first name was uttered are examples of stimuli requiring effortless processing. Participants could, of course, report all of the same properties and much more about the attended speech. These observations constitute the first pieces of evidence that attention controls perception. This type of task also shows that attentional resources are limited. The same effects were shown in the visual modality using two overlapping films (Neisser & Becklen, 1975).

More recently, creative productions such as the Invisible Gorilla video (<https://www.youtube.com/watch?v=vJG698U2Mvo>, Chabris and Simons, 2010) have continued on this line. They show that stimuli falling directly on the center of the retina (the fovea, where visual processing is most efficient; Anton-Erxleben and Carrasco, 2013) can be completely ignored if attention is focused on another type of visual stimulus. In the Invisible Gorilla example, the viewer is focused on white objects and must ignore black ones, rendering him blind to the salient black gorilla right in the middle of their visual field. Similar effects of attention occur in all sensory modalities: this modality-transcending property of attention suggests that although attention is closely tied to perception, it is truly separate from perception. Attention constitutes a cognitive function of its own.

1.2.3.2 Cueing paradigms

With the use of cueing paradigms, attentional testing using behavioral measures became truly systematic. Attentional cues are sensory stimulations, typically short in duration, designed to capture the observer's focus or suggest a target for it. Posner (1980) set the foundation for systematic attentional testing by defining and categorizing different types of cues. His account allowed a thorough investigation of the different processes of attention. He separated general alertness (probed using neutral, non-specific cues) from attentional "orienting" to certain elements, using specific cues in the form of small visual objects flashing at one location or arrows pointing to one spatial area. Since then, cueing has also been used to direct participants' attention to features (Blaser et al., 1999; Lu & Sperling, 1995) instead of locations.

Posner defined "alertness" as a more general state of attention, mainly carrying temporal information (when to expect a stimulus) with perhaps a very general spatial component (e.g., "pay attention to the screen, but not outside of it"). He established a vocabulary to study the relationship between spatial attention and eye movements ("overt" spatial attention means eye

position matches attentional focus, whereas "covert" attention means the eyes do not move according to attention shifts). Importantly, he further divided spatial attention into two additional categories.

"External" attentional cueing used peripheral stimuli to capture participants' attention irresistibly, i.e., automatically. We now call this first type *exogenous* cueing. Posner and others have shown that exogenous cueing enhances performance in a subsequent perceptual task at that location (e.g., detection of a target, discrimination of line orientations), but only for a short duration. Within this short window, accuracy is improved (higher percentage of correct responses), reaction time is shortened, and sensitivity is enhanced (measured using methods from signal detection theory). The reverse effect occurs when the target appears at a different location from the cue: in these "invalid" trials, responses are slowed and accuracy falls (Nakayama & Mackeben, 1989).

"Central" control involved presenting a cue at the observer's fixation point to indicate where to direct their focus, this time voluntarily. Today, this cueing is termed *endogenous*. Voluntary orienting takes time, so improvements on perceptual tasks begin later than with an exogenous cue but also last longer. Endogenous attention is also flexible, unlike exogenous attention. The idea of an "attentional spotlight" was popularized following experiments testing endogenous spatial attention, in which participants could efficiently direct their attention to one specific spatial location and show drastic improvements in performance at the attended location (Giordano et al., 2009).

Cueing paradigms necessarily involve a memory component, because the participant must remember what the cue indicated. Therefore, attentional effects cannot be disentangled from memory ones with cueing alone. However, by comparing valid to invalid trials, the memory component is subtracted out because it should, in principle, be the same between both conditions (if, of course, everything else is kept constant). Attentional effects also occur early (typically in the first 400 ms after cueing; Egeth and Yantis, 1997) whereas working memory is deployed more slowly (usually over 500 ms; Silberstein et al., 2003), so early effects may be attributed to attention.

Cueing also works even after the stimulus has disappeared. This phenomenon has been termed retroactive attentional cueing or simply post-cueing. Sperling (1960) showed that if a subpart of the visual array is cued immediately following stimulus presentation, that portion is typically reported perfectly, whereas its report is generally degraded in the absence of the post-cueing. Retro-perception paradigms ("perceiving in the past") have shown that forcing attention to become focused on a past stimulus, with a cue presented up to 400 ms posterior to stimulus presentation, could lead to the detection of a stimulus that would not have been perceived otherwise (Dugué et al., 2020, 2017a; Nobre et al., 2004; Pestilli et al., 2011; Sergent et al., 2013; Vogel et al., 2005).

1.2.3.3 Visual search

Following the surge of experimental and theoretical proceedings around the topic of attention in the 1970s, Schneider and Shiffrin (1977) defined the properties of automatic vs. controlled processes, and from there, researchers took a keen interest in this dichotomy. Most automatic processes seem to require training, like riding a bicycle or playing an instrument. However, exogenous attention is an example of an automatic process that is not learned, and is opposed to endogenous attention, a controlled process that requires voluntary effort. Following these considerations, one type of attentional task termed "visual search" became widely used to study attentional capture, object salience, and, more generally, perceptual processes. Treisman and Gelade (1980) set the standard for visual search paradigms, in which the participant is asked to search for a specific object or feature(s) among other objects (such as a circle among squares or a vertical bar among horizontal ones; for an example see Figure I.1.2). The visual modality is

avored over other senses because it is the most developed in humans and thus the most studied in the cognitive literature.

Visual search experiments have been instrumental in explaining attentional capture, i.e., how and why certain stimuli can "grab" our attention automatically whereas others cannot. Some combinations of features are easy to detect, while others are hard to extract from the array (Carrasco, 2011). As we will see in detail in Chapter II on the brain dynamics involved in this type of perceptual-attentional task, multiple theories have been deployed to explain some seemingly paradoxical results from visual search tasks (Treisman, 1998; Wolfe et al., 1989).

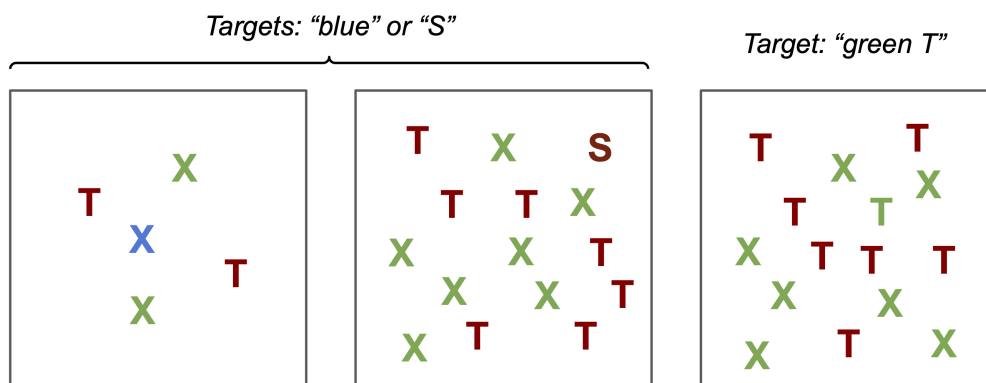


Figure I.1.2: Examples of visual search arrays used in Treisman and Gelade (1980) (recreated from textual descriptions). The participant's task is to search for the target and indicate whether it is present or absent from the display as quickly as possible. In these three examples, the target is present.

1.2.3.4 Which perceptual properties does attention affect?

Attention was found to improve perception in all modalities, and its specific effects on vision are multifold. For example, attention increases the rate of detection of fine details, such as small gaps in visual objects, e.g., a line (Shalev & Tsal, 2002) or a Landolt C (a stimulus borrowed from advanced visual experimentation; Golla et al., 2004). Aside from general perceptual improvement, the main subdivision to test the influence of attention over perceptual ability has been spatial vs. feature- or object-based attention. In terms of spatial attention, which has received more focus overall, it is now well established that it may modulate performance on perceptual tasks. The visual location receiving focalized attention benefits from improved spatial resolution (Carrasco et al., 2006, 2002; Carrasco & Yeshurun, 2009; Golla et al., 2004; Montagna et al., 2009; Yeshurun & Carrasco, 1998, 1999) and texture segmentation abilities (Yeshurun & Carrasco, 2000), as well as reduced masking and crowding effects (Carrasco & Yeshurun, 1998; Shalev & Tsal, 2002; Yeshurun & Rashal, 2010). Aside from perceptual improvements, spatial attention has been found to affect the subjective appearance of visual stimuli (Carrasco et al., 2004, 2006), such as the perceived size of objects (Anton-Erxleben et al., 2007) or their perceived shape (Fortenbaugh et al., 2011). Attention can also alter spatial frequency perception (Abrams et al., 2010; Gobell & Carrasco, 2005) and was shown to modulate the perceived spatial separation between objects (Suzuki & Cavanagh, 1997).

Attention is not exclusively spatial: for example, we can focus on a certain shape in our environment (e.g., rectangles) or a particular color (e.g., white). In that case, we are not selecting any one location in particular, as these object features may *a priori* be found anywhere in our visual field. Object-based attention has been shown to modulate our performance in detecting or discriminating targets much the same way spatial attention has (Egly et al., 1994; O'Craven et al., 1999). When we choose to attend to one specific feature, such as a color, that property becomes prioritized in our visual system, and this enhancement can drastically change our

perception of a stimulus (Blaser et al., 1999). Moreover, certain stimuli capture our attention simply from their incongruity within the environment (e.g., a loud sound in a quiet room, or a pink flower in the middle of a grassy green field). In those cases, although the salient stimulus causes us to orient to its location, the initial capture has little to do with space and more to do with the difference between it and the rest of the scene. Experiments on feature-based attention are less abundant, but many improvements have been found for attended features, such as line orientation, color, direction of motion (Boynton, 2009; Carrasco, 2011; Haenny et al., 1988; Martinez-Trujillo & Treue, 2004; Yantis, 2000) and even whole objects (Chen, 2012; Kahneman et al., 1983; Neisser & Becklen, 1975).

In short, attention is an essential cognitive function that shapes perception, not only by enhancing it when needed and quieting unimportant distractors but also by providing us with a highly efficient, selective, and flexible tool to navigate our complex and constantly changing world. The behavioral effects of attention have now been measured countless times in abundant proof of its necessity for optimal cognitive functioning.

1.3 Cognitive modeling

Once an effect has been measured and explored to some degree, a crucial step toward truly understanding it is to create a model. Almost everything we believe we know about the world is, in fact, a model. When humans first noticed that the sun "rose" in the east and "set" in the west, they assumed that the sun spun around them, as this was the most parsimonious explanation of what they observed and felt, i.e., that the ground did not move. This model of the world worked well until physical measurements disproved it. Physicists then built a new model to take those results into account. This process repeated each time we added new measurements until we reached our current, refined but nonetheless theoretical, model of the solar system. The need to model our reality is mainly due to our limited perceptual abilities: we are at the mercy of our senses, which only capture a limited portion of the information available from the physical world. We can extend this capacity by developing tools for measuring the world, but here too, we are at the mercy of currently available technology. Because we cannot perceive the whole of reality, we fill the gaps in the available information and imagine how the machinery might work.

The mind is a piece of enormous machinery itself, and measuring it may be even more arduous than probing the physical universe. Therefore, modeling its processes is of the utmost importance to test our intuitions regarding how it operates. Cognitive models are hypothetical representations of cognitive processes that explain collected measurements and provide testable predictions about how an individual would behave. Models answer questions about cognition: although they can never be entirely faithful to reality, they give us important clues about general psychological and cognitive functioning. Importantly, they tell us how cognition does *not* work, and can be updated and refined based on actual experimental data to yield more accurate models over time. In particular, modeling the psychological mechanisms of perception and attention has supplied essential tools to understand its characteristics and how cognition operates.

1.3.1 Classic models of perception and attention

By most accounts, the first major cognitive model of attention came from Broadbent (1957), who proposed a model of "early selection" and "filtering," also termed the "bottleneck model of attention." According to Broadbent, we only treat the information that we are currently paying attention to; anything else is ignored to the point of not being processed at all beyond the sensory entrance (Broadbent, 1957, 1982). This bottleneck model of attention was challenged by

Treisman (1960). Using a dichotic listening task, she showed that a participant could repeat the speech heard in one ear but switch involuntarily and without even noticing it to repeating the speech in the other ear, if the semantic information flowed naturally from the initially attended ear to the initially ignored one. This result, which subsequent experiments have reinforced (Deutsch & Deutsch, 1963; Norman, 1968), showed that processing was occurring outside of the attentional focus to a high level (i.e., extracting semantic meaning from the speech).

Following Broadbent, Kahneman (1973)'s model of attentional resource distribution proposed that the principal contributor to processing efficiency is attentional effort, which in turn is influenced by the individual's current state (wakefulness, motivation). This model extended explanatory power to some of the results found up to that time, which could not be explained by Broadbent (1957)'s bottleneck model.

Another early example is Wickens' model of separate reserves (Wickens et al., 1984), according to which the different aspects of the task (e.g., sensory modality, spatial vs. feature, motor vs. semantic response) constitute different "dimensions" of the attentional resource reserve. For example, driving requires attentional allocation towards visual processing and limb movements. On the other hand, chatting with a passenger taxes verbal processing and facial coordination. If two tasks tax the same subcategory in one dimension, they will interfere with each other. This representation neatly explains why it is relatively easy to drive while conversing with a passenger, but not while texting, which taxes much of the same resources as driving. This model also yielded testable predictions about which pairs of tasks would or would not be performed simultaneously with ease.

Over time, models become better-informed thanks to past theories augmented with new data. We can model more and more precise mechanisms of attention, e.g., Blaser et al. (1999)'s model of attentional salience in illusory motion. This model separates object perception from salience in two parallel processing pathways. It explains why, when we attend to one color at the expense of another, we do not perceive the colors themselves as different: the ignored one does not appear as a weaker shade, nor does the attended one become more vivid, but it is enhanced to the point of reversing the direction of apparent motion.

1.3.2 Two-stage models of visual search

How exactly might the visual system handle a visual search? Hoffman (1978, 1979) introduced the idea of a two-stage model of visual search, making it the first in this category. Two-stage models represent visual search in two separate steps: a first, rapid stage of feature categorization, and a second, slower stage of object recognition. From Hoffman's initial suggestion, other groups joined the search for the cognitive mechanisms underlying visual search.

When they set the standard for visual search tasks, Treisman and Gelade (1980) also set the standard for cognitive modeling of the processes underlying visual search. They presented the "Feature Integration Theory" (FIT) to explain the results found in these tasks. The FIT model posits two main steps towards identifying the target during visual search: first, a decomposition of all the attributes (features) present on the screen, in parallel (this step alone is enough to identify a unique feature of the target, or its absence, in an easy search). The second step consists in binding all attributes for each item, which must be performed serially (one item at a time) to compare each combination of features to the searched one. This process iterates until the combination matches the searched one and the target is found. This model also provides a mechanistic explanation to the theory of periodic attentional sampling (see next section).

In turn, Wolfe et al. (1989)'s model takes inspiration from both Treisman and Gelade (1980)'s proposition and Hoffman (1978)'s inclusion of a guiding link from the first stage to the second. In this third version of the two-stage model of visual search, the first stage creates a "map" of the item locations. Those holding the most features in common with the searched item get assigned the highest saliency value, allowing the second stage to restrict its search among the most

salient items. Many of the results viewed as exceptions under Treisman and Gelade (1980)'s FIT framework are accounted for under this modified version.

More recently, the strict form of FIT was rejected because it became unable to explain too many "exceptions." The initial FIT model postulated a strict dichotomy between "parallel disjunctive" and "serial conjunctive" search. A parallel disjunctive search occurs when the target has a unique feature not present in the distractors, and all items are therefore processed at once. In contrast, items are processed individually if the target shares any features with the distractors, constituting a serial conjunctive search. Under this framework, the two forms of processing do not overlap or inform each other at all.

Atkinson et al. (1969), Townsend (1990), Wolfe (1998), and Wolfe et al. (1989) showed that this model could not adequately reflect cognitive processing, based on two main points. The first is that, in establishing this dichotomy, FIT effectively ignored the importance of spatial relations between items, which can strongly impact individual object salience. The second is that FIT dismisses specific relations between features (e.g., orientation) that other feature types (e.g., color) do not share. It also seems sufficiently evident that if item features are difficult to parse independently of their arrangement, they will not pop out even in the case of a unique feature. To illustrate this, we can picture a search setup in which the target is a grating (a visual stimulus composed of straight bars) that is only very slightly oriented clockwise from vertical (at the Just-noticeable orientation of 0.5°), and the distractors are similarly slightly counter-clockwise oriented gratings. Although the target has a unique feature (clockwise orientation), it will not pop out, i.e., parallel processing will not suffice to find it.

Despite its limitations, FIT remains the basis for many current ideas of the cognitive processes underlying visual search and has been updated to form one of the dominating modern views of visual search (Koch & Ullman, 1987; Tsotsos & Rothenstein, 2011). This view is infused with the philosophical undertone that attention is fundamentally selective, i.e., that at its core, it is a mechanism allowing for the identification of relevant inputs and facilitation of their continued processing. We will cover this topic in detail in Chapter II.

1.3.3 Periodic cognitive sampling

We have defined attention as the psychological process by which the cognitive system selects relevant information among the enormous amount of stimulation that enters it at any given moment. Similarly, perception itself is an immensely complex operation by which information from the external world, such as photonic wavelengths, is converted to signals and translated to a language our psyche may understand and manipulate. Perception and attention are enormous cognitive tasks that use up a large portion of available resources. Can the system filter information constantly over time, without any periods of lowered efficiency? Experimental evidence from behavioral studies in humans suggests that this is not the case.

Tracking performance over time after resetting attentional capture with a sensory stimulus reveals behavioral periodicity (Landau & Fries, 2012). Experiments in this field typically probe performance with behavioral measures (e.g., reaction time, accuracy) while neural (Dugué et al., 2016) or sensory (Dugué & VanRullen, 2014; Huang et al., 2015) perturbations are delivered at definite temporal intervals, revealing the time course of perceptual and attentional deployment (for review see Kienitz et al., n.d.). Selective attention was found to perform temporally periodic sampling of the visual scene (Senoussi et al., 2019; for review see: Dugué and VanRullen, 2017; Fiebelkorn and Kastner, 2019; Kienitz et al., n.d.), suggesting that it relies on innately periodic processes (VanRullen et al., 2007). Similar findings with more fundamental perceptual manipulations reveal periodic fluctuations in perception as well (Michel et al., 2021; for review see: Gaillard and Ben Hamed, 2020; VanRullen, 2016b). In particular, low frequencies in the theta, alpha, and low-beta bands (4-20 Hz) are most prominent in these behavioral fluctuations (Song et al., 2014), making them the best candidate for a cognitive sampling rhythm.

The evidence clearly suggests that cognitive sampling is not constant over time. Instead, perception and attention seem to undergo periodic episodes of enhanced and lowered efficiency, which may successfully offload some of their processing weight and avoid a neural burnout (VanRullen, 2016b). This periodic sampling model is currently the most parsimonious in its account of the experimental data presented above.

Cognitive modeling fills the gaps in knowledge left by limited measures of behavioral functioning. Theoretical frameworks of cognitive mechanisms have been especially useful in the study of attention, which has proven to be quite a complex function and decidedly will not allow itself to be considered in a simple, unified manner. Early models defined attention as a cognitive resource bottleneck, but this view was soon refined. Two-stage models of visual search posit detailed cognitive and neural mechanisms during cognitive processing. Finally, the periodic sampling theory hypothesizes that attention and perception are deployed in a rhythmic manner and rely on periodic neural processes. How do these theories hold against more precise measures of the brain itself?

2 Attention in the primate brain

With the rise of technology and the rapid advancement of neurophysiological tools applied to measuring the brain, our capacity for describing neural processes has exploded in the last decades and allowed for the characterization of more and more complex cognitive operations. Thanks to this progress, we now rest upon an immense body of literature demonstrating the various effects of attention inside the brain and its possible implementation in terms of physical and computational mechanisms.

2.1 Neuroimaging

2.1.1 Origins of electroencephalography

If we wish to know anything about the brain mechanisms giving rise to behavior, we must measure the brain. Today, it is not possible to physically probe a human brain if its owner does not present severe neurological symptoms, such as epilepsy or cancer. To circumvent this problem, neuroscientists and engineers continuously develop tools that allow us to estimate what occurs under the skull of healthy individuals. These measures are necessarily some levels removed from subdural mechanisms, but they give us valuable clues on human brain functioning. The first major tool used to record the brains of healthy humans was the electroencephalogram (EEG), for which we now provide an overview.

Why was the electroencephalographic signal recorded initially? Richard Caton, an English doctor practicing in the late 19th century, had gathered from measurements with galvanometers of animal brains that electric currents seemed to emanate from the surface of the cortex. He set out to record this electric activity in rabbits and monkeys and was the first documented person to find that the measured electric currents correlated with the functional state of the gray matter (motor and visual: Caton, 1875).

In 1890, Adolf Beck extended Caton's studies and found that the electric activity in the brains of recorded animals showed periodic fluctuations over time, thus reporting the first account of brain waves (Coenen et al., 2014), which we will refer to as "oscillations" from here forward. Like any other type of wave, brain oscillations are characterized by three main properties: frequency, amplitude, and phase. These are illustrated in Figure I.2.1.

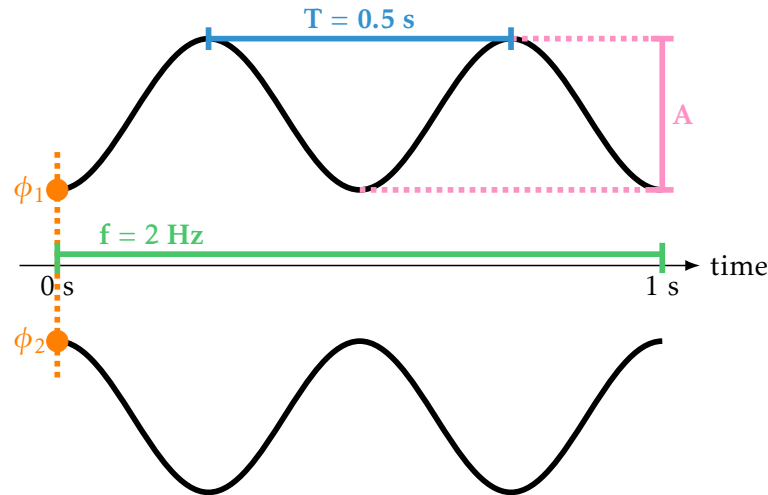


Figure I.2.1: Illustration of the three main wave properties. Frequency (f , in green): in this example, one second in time contains 2 wave cycles, so the wave has a temporal frequency f of 2 Hz. It is the inverse of the period (T , blue, also called wavelength λ): $1/T = 1/\lambda = 1/0.5 \text{ s} = 2 \text{ sec}^{-1} = 2 \text{ Hz}$. Amplitude (A , pink): the height of the wave, expressed in the unit of the phenomenon being measured (in the case of EEG measures this is typically microVolts, μV). Phase (ϕ , orange): the top and bottom waves have the same frequency and amplitude, but the top one starts at a trough (instantaneous phase ϕ_1) and the bottom one starts at a peak (instantaneous phase ϕ_2). Thus, the point along the cycle of one is always the opposite of the other, a relationship termed "anti-phase".

The frequency (f) is typically reported as the number of cycles per second, i.e., Hertz (Hz). It is the mathematical inverse of the duration of one cycle, called the period (T) or wavelength (λ). The amplitude (A) is the measure taken between peak and trough values, giving the "height" or "strength" of the wave. This measure is often given in the form of power, which is the square of amplitude (therefore usually given in units of squared microVolts, μV^2). Finally, the phase (ϕ) represents the point along the cycle (peak, trough, or any point in between) at which the wave started. While discussing instantaneous phase, it represents this point along the cycle at a particular moment in time.

In 1912, Vladimir Pravdich-Neminsky recorded the very first evoked potential (EP) in a mammal (a dog; Pravdich-Neminsky, 1913). This finding gave rise to an entire branch of study in neuroscientific research. From there, EPs were extended to human measures and became a widespread analysis method in neuroscience. Evoked response potentials (ERPs) are time- and phase-locked activity, i.e., bursts of activation with the same polarity across trials that always happen at the same time relative to whichever event the experimenters lock to (usually stimulus onset). They provide a "second window" into brain functioning and its relation to cognition and constitute an additional guide for behavioral measures (Hillyard & Kutas, 1983). ERPs have been instrumental in neuroscientists' quest to understand the brain and have been linked to many cognitive processes (for review see Kok, 1997). However, spontaneous "noise" typically has a much larger amplitude than the evoked signal (Nunez & Srinivasan, 2006). Therefore, by definition, ERPs average all of the information together to remove any spontaneous activity and

leave only the repeated, evoked signal. We will review how spontaneous oscillations may also convey crucial information. Furthermore, averaging the signals causes a loss of the distinction between amplitude and phase effects (Cohen, 2014). As we will see in Section 3.1, distinguishing the effects of the different properties of oscillations is crucial to obtain a solid understanding of how neural mechanisms give rise to cognition.

First findings in human electroencephalography One century ago, the German doctor and neurophysiologist Hans Berger was searching for the brain properties giving rise to psychic phenomena, and he noticed something that changed the course of neuroscience to this day. Not only was he the first to place electrodes on a human's scalp to record the electric currents from the brain, giving birth to the "electroencephalogram" or EEG (Haas, 2003). He also discovered that, when people close their eyes, a clear wave appears in the time course of the electric signal emanating from their brain and that this temporal wave disappears when they open their eyes (Berger, 1929). This was the first account of the cerebral alpha rhythm (7-13 Hz), soon confirmed by Adrian and Matthews (1934), who also reported prevalent alpha activity in the occipital area. With this new and easily adaptable technology available, many other groups could record EEG for their distinct research interests. Following in Caton and Berger's footsteps, Bishop (1932) applied EEG to the rabbit cortex and found cyclic electrical fluctuations in the projections between the retina and the occipital area, which he interpreted as reflecting a periodic alternation of cortical excitability.

The alpha rhythm is easy to see in human EEG during rest, so it was originally thought of as an "idling" rhythm (for review see Pfurtscheller et al., 1996), but its role has since been characterized in more detail. Indeed, brain oscillations from each band can show very different correlations to behavior depending on which area they are recorded from, as revealed by intracortical recordings (Başar et al., 1997), so the generalities made here should not be taken at face value. Aside from the alpha rhythm, Hans Berger also reported the beta rhythm (13-30 Hz) emanating from the primary motor cortex (Berger, 1931). Beta oscillations have widely been confirmed to occur during "readiness" (preparation) for a movement (Wang, 2010). Over time, EEG became of particular interest to epilepsy research, mainly for clinical purposes, but this allowed for the characterization of other frequency bands and their relation to various cognitive phenomena during normal functioning. The gamma band (30-100 Hz) has been observed all over the cortex and may serve to synchronize neuron networks for various cognitive tasks (Lopes da Silva & Niedermeyer, 2005). Very low frequencies have also been reported: the theta rhythm (4-7 Hz) was also originally thought to indicate idling, and with ERP studies was mainly associated with cognitive suppression, i.e., the voluntary repression of an action by the individual (Kirmizi-Alsan et al., 2006). Finally, the slowest rhythm to be correlated with cognitive functioning is the delta band (1-4 Hz), a prominent component during sleep (Iber et al., 2007).

Electroencephalographic activity clearly correlates with cognitive functioning. Neural signals recorded via EEG consistently form patterns as a reaction to certain events, and a broad range of frequencies seems to emanate from the human cortex that change according to cognitive tasks. What do we know about the brain mechanisms that might give rise to such signals?

2.1.2 What EEG measures and how it informs us about the physical brain

The typical EEG cap consists of 64 or 128 electrodes placed at regular spatial intervals all over the scalp, from forehead to nape on the front-to-back axis and from ear to ear on the coronal axis. Each electrode reads out the signal coming from a corresponding patch of cortex, which then must pass through the skull and scalp, thus averaging about 100 million to 1 billion

neurons (Nunez & Srinivasan, 2006). Whereas intracranial recordings of single neurons or small neuronal populations give a detailed account of micro-scale neuronal activity, EEG provides a "big picture" record of brain activity during cognitive functioning, i.e., a completely different and possibly complementary type of information. This more general measure consists primarily of highly coherent neuronal activity across several centimeters of the cortical surface (see Figure I.2.2) and only when specific neuron orientations amplify the signals by allowing their summing (as on the top of a gyrus), as opposed to entailing their interference (e.g., inside a sulcus).

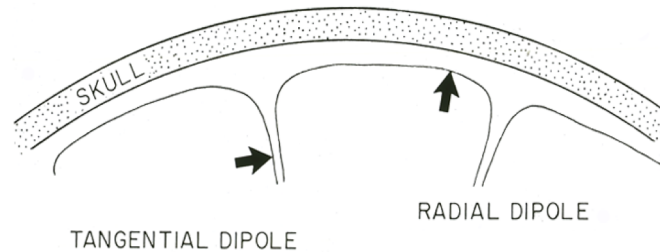


Figure I.2.2: Cortical dipoles. EEG electrodes can record activity from gyrus neurons (radial dipoles), but not from sulcus neurons (tangential dipoles), because the perpendicular currents cancel out across the sulcus. Figure adapted from Cohen and Halgren (2003).

An EEG electrode mainly detects signal from the dendrites of pyramidal cells in the neocortex. These dendrites are present at the superficial layer of the cortex, i.e., closest to the EEG electrode (Fröhlich, 2016). When a dendrite receives an excitatory input, for example from another pyramidal neuron, it creates an electric current (an ion gradient across the receiving cell's membrane) called an excitatory postsynaptic potential (EPSP), which creates a "current sink" (a concentration of negative ions) in the extracellular fluid around the synapse. When many of these are summed, e.g., if multiple excitatory cells send inputs simultaneously, the receiving cell fires an action potential. Neurons can also receive inhibitory input, usually from interneurons using the neurotransmitter GABA, which creates a "current source" (positive ion concentrations) at the synapse and produces an inhibitory postsynaptic potential (IPSP) across the membrane of the receiving neuron. When a local sink or source arises, it is counteracted by sources or sinks, respectively, at more distant locations in the neuron to preserve the law of charge conservation (Nunez & Srinivasan, 2006). This counterbalancing of charge creates dipoles at the level of individual neurons. More importantly for EEG recordings, in many cases, large assemblies of neurons receive synchronized input. Since neurons are generally oriented perpendicularly to the surface of the cortex, i.e., parallel to each other, we are effectively left with a "dipole sheet" that may span a large surface area and thus be detectable by a scalp electrode. Then, the only hindrances are skull and scalp diffusion (volume conduction), which may reduce the signal to one-half and up to one-fifth of its original magnitude in the cortex.

Despite these issues, the signal recorded from scalp EEG was shown to correspond to intracranial activity, as made evident by concurrent EEG and iEEG recordings (Van Der Loo et al., 2007), as well as simultaneous EEG and multi-unit activity (MUA) measures (Whittingstall & Logothetis, 2009). More specifically, the *amplitude* of EEG high-frequency (>24 Hz) components and the *phase* of its low-frequency (1-8 Hz) activity relate to intracortical neuron population spiking. This relationship was confirmed using concurrent EEG and functional magnetic resonance imaging (fMRI) in multiple studies, further showing that gamma power in the EEG reflects excitatory activity (Logothetis et al., 2001; Moosmann et al., 2003; Mukamel, 2005; Niessing et al., 2005), whereas alpha power negatively correlates with fMRI activation (Goldman et al., 2002; Kilner et al., 2005; Laufs et al., 2003; Moosmann et al., 2003).

In the human brain, most connections between neurons are corticocortical, and only a

small fraction are thalamocortical. The fraction of thalamocortical projections is higher in other mammals, perhaps explaining their focus in the neurophysiology literature, which is based mainly on nonhuman animal models. These connections involve delays because action potentials must travel down each neuron's axon, and the signal must pass from one cell to the next via synaptic input. However, these delays (on the order of tens of milliseconds) cannot explain the length of time taken for an event to reach consciousness, e.g., a sensory stimulus, which is on the order of hundreds of milliseconds (Dehaene et al., 2006). This insufficiency of feedforward-only signals to explain cognitive phenomena suggests an important role for feedback connections in cognition, as we have discussed. This observation, combined with the plethora of short- and long-range connections reported between cortical cells, indicates that the interactions between neurons are incredibly complex, making them difficult to model. Electrophysiologists typically speak of "cell assemblies" of different spatial scales to simplify the representation of the cortex. A cell assembly denotes a group of neurons that momentarily acts as a functional unit (Freeman, 1975; Hebb, 1949; Ingber, 1995) and can show a variety of local resonant properties, i.e., different frequencies, amplitudes, and phase (Nunez, 1995). EEG electrodes are thought to measure parts of the dynamics of cell assemblies at macroscopic scales.

2.1.3 Magnetic imaging

Two new machines were recently developed to image the brain: magnetoencephalography (MEG) and magnetic resonance imaging (MRI). Although these two technologies both rely on the properties of magnets at their core, each one uses them very differently and produces distinct results. Whereas MRI has exceptionally high spatial resolution counteracted with inferior temporal precision (on the order of seconds), MEG makes a good compromise between fair spatial localization abilities (2-3 mm on the cortical surface) and high temporal resolution (<1 ms), like EEG (Hämäläinen et al., 1993).

MRI and MEG's operating mechanisms are also very different. MRI applies powerful magnetic fields to tissue and captures electron spins in different atoms, making it possible to detect the borders between matter made from different compositions (Hinshaw & Lent, 1983; Lauterbur, 1973). Initially, this was highly useful to create static images of the inside of the body, akin to an X-ray (Damadian, 1974). More recently, a new use was found for it: the blood oxygenation level-dependent (BOLD) signal enables dynamic capture of blood circulation in the brain, which has been shown to correlate with neuronal activity (the neurons require energy while activating, which is supplied by the blood; Ogawa et al., 1992). This dynamic use of the machine has been termed functional MRI (fMRI).

On the other hand, MEG does not create magnetic fields but captures them, thus measuring sensibly the same cells as EEG, but instead of their electric (perpendicular) components, it captures the magnetic fields emanating from the cortical dipoles, which run parallel to the cortical surface. In other words, whereas EEG captures activity from gyri, MEG mainly measures activity from the sulci, making it an ideal tool to measure primary sensory areas (such as V1), which are located inside these cortical fissures (Hämäläinen et al., 1993).

2.1.4 Complementarity between MEG and EEG

MEG is based on James Zimmerman's "superconducting quantum interference device" or SQUID, a sensitive device to measure the small magnetic currents flowing from the electric transfers in the cortex (Zimmerman et al., 1970). From its early implementation, it could detect the spontaneous alpha rhythm reported by Berger using EEG forty years prior (Cohen, 1972) as well as evoked responses (Brenner et al., 1975). Like EEG electrodes, MEG magnetometers are sensitive to the activity produced by many nearby neurons simultaneously. However, magnetic fields are less prone to volume conduction, so solving the inverse problem of which sources

gave rise to the MEG sensor signal is much easier. Spatial localization is thus highly improved, without a cost to temporal precision (Buzsáki, 2006; Hämäläinen et al., 1993).

Despite its obvious advantages, MEG is a large and complex machine, requiring a costly setup in a large enough room and specially trained operators. These requirements render it more expensive than EEG and inflexible to different environments. With these limitations, MEG is less accessible to laboratories than EEG, especially those with more limited means or performing ecological paradigms that require high mobility.

Therefore, EEG and MEG are both powerful tools yielding different signals from the same cortical sources, with advantages and disadvantages to both. It is clear then that using both in complement presents an ideal way to study the relationship between brain functioning and cognition.

2.2 Neural bases of attention

2.2.1 A bit of anatomy

To understand the neural effects of visual attention, the reader must have in mind a general picture of the anatomy of visual areas in the brain, for which we now provide a quick overview (for an illustration see Figure I.2.3). Photons hit the retina at the back of the eye, which transduces the energetic signal into electricity. Most of the electric signal (~90%) is sent to a critical structure at the brain's center, the thalamus, and more specifically to one thalamic

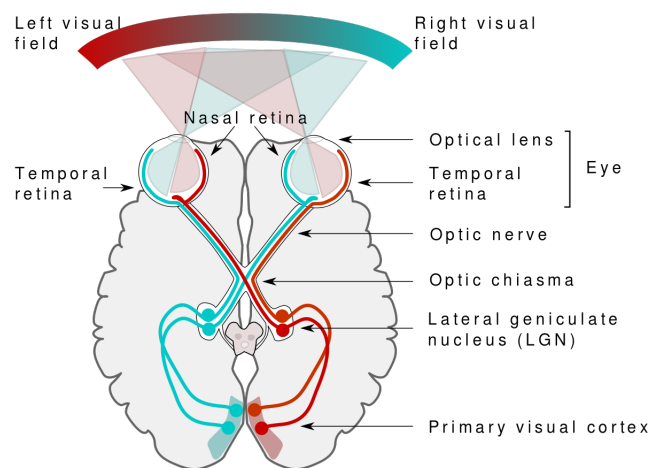


Figure I.2.3: The pathway from the external visual field to the primary visual cortex V1. The left portion of the visual field is projected onto the right hemisphere of V1. For each eye, the nasal retina is the portion of the retina located closest to the nose, receiving input from the outermost portion of the visual field. Conversely, the temporal retina is the portion on the side of the temple, receiving visual information from the opposite side. The optic nerve is an axon fiber projecting from the eye to the lateral geniculate nucleus (LGN) on either side; the two optic nerves cross at the optic chiasma. The LGN is part of a subcortical structure called the thalamus. V1 is located on the occipital lobe, inside a crease called the calcarine fissure. CC 4.0 Miquel Perello Nieto.

region named the Lateral Geniculate Nucleus (LGN, for its bent shape). The LGN relays the information to the back of the brain, onto the primary visual area (V1) or "striate cortex" of the occipital lobe. From there, the pathway depends on the information received and on the

viewer's task: the information can be sent towards the temporal lobe, or "what" pathway, to process the identity of what is in the visual field; or it can be sent up the dorsal route towards the parietal lobe, on the "where" pathway, to extract precise spatial information. As the electric impulses reach further areas along the pathway (see Figure I.2.5), they progressively represent more complex structures, from simple spots of light in the LGN, to oriented bars in the occipital cortex, to much more complex objects such as stars and spirals in V4, to entire faces in the inferotemporal (IT) cortex (Salinas & Sejnowski, 2010). The ~10% that does not go to the LGN journeys to other subcortical structures, including another thalamic nucleus called the pulvinar and the superior colliculus.

Thanks to the pioneering work of Hubel and Wiesel launching the method of receptive field (RF) mapping (Hubel & Wiesel, 1959), strengthened by many other physiological and neuropsychological lesion studies, we now have a relatively clear idea of the "processing pathway" for visual information. RF mapping is the method of recording the activity from a neuron while presenting stimuli at various locations in the visual field or with various properties, and determining which location in space or which stimulus properties that cell responds to maximally (its "tuning"; see Figure I.2.4). This tuning defines a spatial receptive field and, if applicable, a preferred property (e.g., preferred orientation).

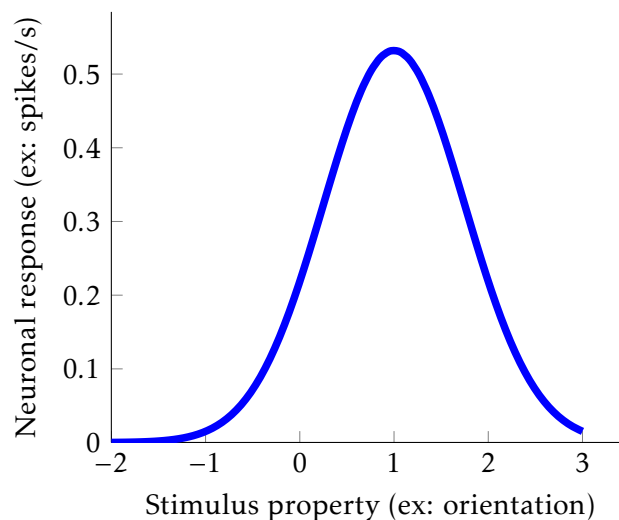


Figure I.2.4: Example of a neuron's tuning curve. The neuron is selective for the property at which its response peaks: in this case, the spiking rate is maximal at an orientation of 1, so the neuron is said to be selective for that orientation.

2.2.2 Attention modulates processing in sensory areas

Attention modulates perception in behavioral measures, so the overarching hypothesis in the neuroscientific study of attention is that attention would directly affect neuronal processes in sensory areas. The following are a few highlights of this rich literature to show how attention can modulate the visual pathway, from low-level processing regions to areas implicated in the extraction of highly complex information. We encourage the reader to refer to Figures I.2.5 and I.2.7 as they summarize the regions and relations presented throughout this section.

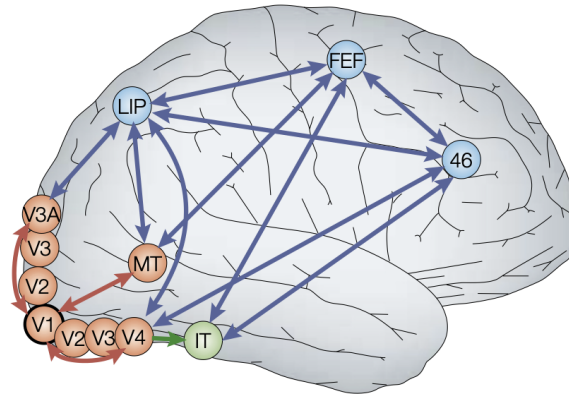


Figure I.2.5: The visual network in the human brain. Striate and extrastriate areas are in red. The inferotemporal cortex (IT) is in green. Fronto-parietal attentional areas are in blue. V1: primary visual cortex. MT: middle temporal cortex. LIP: lateral intraparietal area. FEF: frontal eye fields. Reproduced from Tong (2003).

2.2.2.1 Early visual processing: thalamus to V3

Thalamus and low-level occipital cortex: neurophysiological recordings Vanduffel et al. (2000) seem to be the first group to have found that the lateral geniculate nucleus (LGN) is modulated by attention, enabled by an unusual technique of mapping glucose uptake from brain slices. Specifically, they found that magnocellular layers of the LGN were more metabolically active when the animal was attending to a large central stimulus than when they attended elsewhere, to its sides. These magnocellular layers contain cells responsible for the processing of large spatial resolution and movement (Denison & Silver, 2012). Notably, the layers of V1 receiving direct input from those LGN layers show the same attention-dependent activity modulation, suggesting that the modulation propagates through the visual system from the earliest relay. Vanduffel et al. (2000) and McAlonan et al. (2000) both also found that the thalamic reticular nucleus (TRN), an area of the thalamus that also relays to the cortex in the rat brain, showed more robust activation in the area associated with an attended stimulus than the area associated with an unattended one.

Early studies of the effect of attention on the primary visual cortex (V1) yielded contradictory results, and when they did support attentional modulation, the effects were quite small (Haenny & Schiller, 1988; Luck et al., 1997; Motter, 1993). However, more recent studies found convincing attention-related facilitation (Vanduffel et al., 2000, see above) and inhibition in primate V1 (Mehta et al., 2000a,b).

Luck et al. (1997) tested spatial attention in V2 extrastriate cells and found that attention favors the response for the attended stimulus. They deliberately arranged multiple visual stimuli to fall within the same large receptive field (RF) of single extrastriate V2 neurons. Thanks to this manipulation, they confirmed that attention favored one stimulus only when two stimuli fell inside the same RF; otherwise, there was no favoring. They interpret this result to mean that attention enhances competition between neighboring stimuli, because when only one stimulus falls inside the RF, there is no need for competition.

Although competitive neuronal mechanisms had been reported previously in various areas, the view of competition within the receptive field mainly comes from Reynolds et al. (1999). They showed that when two stimuli are presented within the same RF, the cell's response is not equivalent to a sum of the responses from the individual stimuli (when presented alone). Instead, it corresponds to a weighted average of the two responses. This finding led to the interpretation that stimuli cannot be processed independently inside a single RF; on the contrary, they interfere and mutually suppress each other.

Reynolds et al. (1999)'s evidence shows that attention may bias processes down to the response of single neurons, if their RF includes the attended item(s). V2 neuronal responses to two stimuli behave as if only the attended stimulus is presented, whereas usually (without attention), it would respond as a mix of the two individual responses.

Mehta et al. (2000a,b) suggest that one of the attentional effects on sensory areas is to reduce the mutual inhibition between neighboring cells, thus enhancing competition and an "attentional on-center, off-surround" effect. Just as in V1, the effects of attentional enhancement were found to increase firing for all orientations proportionally, i.e., they do not "sharpen" or "broaden" the neurons' tuning curves (McAdams & Maunsell, 1999).

Area V3 is rarely mentioned because it has changed substantially in definition over time. The area initially defined as V3 contained heterogeneous subdivisions and was cut into areas "dV3" (dorsal) and "VP" (ventroposterior). However, soon VP was no longer considered part of V3 (Clarke & Miklossy, 1990). Because of these inconsistencies in terminology, we do not discuss V3 further.

Attention modulates low-level sensory areas: support from human neuroimaging We have now seen how attention is tested in animal models to precisely describe its neuronal effects on low-level visual areas. Evidence from EEG, MEG and MRI recordings in healthy humans confirms these early processing findings.

An early electro-retinal recording in humans reports that attention modulates activity as early as the eye itself (Eason et al., 1983). Activity in the human LGN is also modulated by attention (Kastner et al., 1998; O'Connor et al., 2002). Attention experiments under fMRI revealed that this first relay of visual information enhances baseline activity and suppresses responses to ignored stimuli (for review see Kastner & Pinsk, 2004, p.484-488). Functional magnetic imaging also allowed a proper investigation of attentional modulation in V1, which was difficult to attain previously from its localization inside the calcarine sulcus (Kanwisher & Wojciulik, 2000). fMRI provided abundant proof that V1 is also modulated by attention using novel paradigms (e.g., Bahrami et al., 2007) and tasks that resembled those presented to nonhuman animals (Gandhi et al., 1999; Somers et al., 1999; Watanabe et al., 1998). Similar attentional modulations were found in humans from V1 to V3 (Buracas & Boynton, 2007; Martínez et al., 1999).

As illustrated in Figure I.2.6, the visual field is represented retinotopically in the visual cortex, i.e., the 2-dimensional spatial relations resulting from the projection of external light onto the retina are maintained in the neural space. In other words, if two points are adjacent in the visual field, they will project to adjacent neurons in the visual cortex (Brefczynski & DeYoe, 1999; Hubel & Wiesel, 1962; Orban, 2012; Sereno et al., 1995). In vision experiments, retinotopic mapping can be seen as an approximation to receptive field mapping in animal models, in the sense that visual stimuli are presented to the participant while their brain is recorded (this time with fMRI), and the location in the visual field is mapped onto the occipital cortex. Astonishingly, the same results can be obtained simply by attending to points in the visual field, instead of presenting physical stimuli at those locations (Brefczynski & DeYoe, 1999).

Globally, the baseline activity in the occipital cortex was found to decrease overall for unattended locations compared to when attention was diffuse across the visual field (Smith et al., 2000). Furthermore, different sub-types of attention (endogenous, exogenous, pre-cued, and post-cued) show different patterns of modulation in the occipital cortex (Dugué et al., 2020). These results were found thanks to fMRI retinotopic mapping methods.

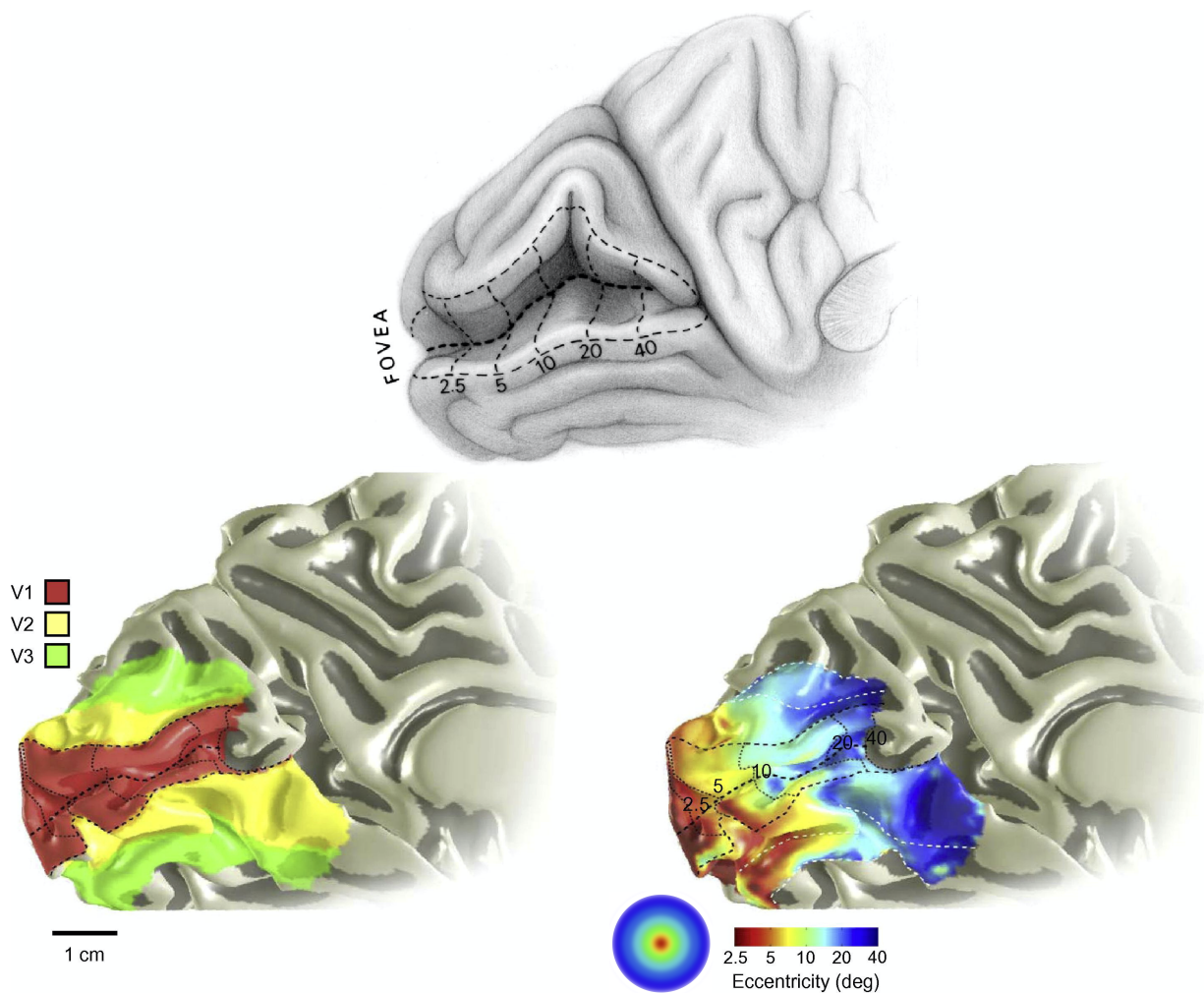


Figure I.2.6: The visual field projects onto the primary visual cortex retinotopically. Top: estimated V1 eccentricity map deduced from lesion data (Horton & Hoyt, 1991). Bottom left: arrangement of V1, V2, and V3 in the human occipital cortex. Bottom right: eccentricity map as measured by fMRI retinotopic mapping. The image seen in the visual field (circle inset) is mapped onto V1 with the same spatial organization. Distortions due to cortical magnification magnify the fovea (red). Figure adapted from Wandell and Winawer (2011).

2.2.2.2 Intermediate visual processing

V4, IT, and MT in neurophysiological recordings Area V4 seems to be the first along the visual pathway to perform intermediate-level sensory encoding. Its neurons retain basic visual characteristics, such as tuning curves to stimulus properties (McAdams & Maunsell, 1999). However, it is also involved in higher-level processing such as form recognition and visual search, including attentional filtering (enhancement of relevant information and suppression of irrelevant elements; Kastner & Pinsk, 2004; Treue, 2014).

Numerous studies show a neural influence of attention in V4 independent of spatial location (Bichot et al., 2005; Haenny et al., 1988; Haenny & Schiller, 1988; Maunsell et al., 1991; Moran & Desimone, 1985; Motter, 1993, 1994; Spitzer et al., 1988), suggesting that neural modulation in this area can directly support feature-based attentional effects in behavior. The inferotemporal (IT) cortex, a visual processing area known to play an important role in object recognition

(DiCarlo et al., 2012), also reflects feature-based attention (Chelazzi et al., 1998, 1993, 2001; Sato, 1988). V4 and IT also show simultaneous facilitation for attended stimuli and suppression for unattended ones, i.e., filtering (for a review see Kastner & Pinsk, 2004, pp.488-493).

Several studies took advantage of the middle temporal area (MT)'s specialized motion processing (Britten, 1996) to show that neurons with RFs outside the focus of spatial attention still show significant modulation by feature-based attention (Martinez-Trujillo & Treue, 2004; Saalmann et al., 2007; Treue & Martinez-Trujillo, 1999; Treue & Maunsell, 1996). Interestingly, no sustained increase of firing is observed in MT neurons while the monkey attends inside the RF, which we would expect if attention raised cell excitability, as is found in V4 cells (Chelazzi et al., 1998; Luck et al., 1993, 1997). This distinction suggests that MT performs processing at a more complex level than V4, and may comprise one of the earliest areas to participate in attentional control.

In terms of spatial attention, there seems to be a steady consensus around the model of receptive fields presenting on-center, off-surround dynamics in intermediate-level visual processing areas (Recanzone & Wurtz, 2000; Treue, 2014; Womelsdorf et al., 2006). These results join a body of evidence indicating that V4 neurons exhibit intra-RF competition, like lower-level areas (Luck et al., 1997; Mehta et al., 2000a,b; Reynolds et al., 1999). Beyond single RF enhancement, RF mapping with high spatial resolution revealed that shifting attention across the visual field caused RFs in V4, IT and MT to stretch and shift towards the attended location (Anton-Erxleben et al., 2009; Connor et al., 1996, 1997; Moran & Desimone, 1985; Niebergall et al., 2011; Womelsdorf et al., 2006). These findings suggest that the behavioral effects of attentional enhancement rely at least in part on receptive field shifts.

Single-neuron measures may not suffice to describe the neural effects of attention. A revisiting of attentional effects using local field potentials (LFPs), a measure of population-level dynamics, showed that attention effectively sped up V4 and MT neural responses at the population level (Galashan et al., 2013; Sundberg et al., 2012). This neural speeding may directly influence the reaction times of individuals when attending to the proper location or feature, thus providing part of the explanation for the behavioral speed improvement. Two additional papers (Cohen & Maunsell, 2009; Mitchell et al., 2009) showed that changes in individual V4 neurons only held marginal explanatory power for the increase in psychophysical sensitivity that is observed behaviorally. Instead, they showed that a decrease in variability at the level of populations of neurons almost fully accounted for the improvement. These novel findings show highlight the importance of studying cognitive processes at every level of scale, from micro- to macroscopic.

Attentional modulation in intermediate visual areas: support from neuroimaging Early fMRI studies confirmed that attending to one stimulus suppresses responses from nearby stimuli (Kastner et al., 2001, 1998), suggesting that the competitive mechanism of on-center, off-surround also takes place in the human cortex. Separate studies have confirmed that attention enhances activity in intermediate visual cortical areas as well as the temporal components of EEG evoked responses at occipital electrodes, including in anticipatory attention devoid of any physical or sensory stimulation (Kastner et al., 1999; Luck & Girelli, 1998; Martínez et al., 1999). MT activity in humans was also found to be modulated by attention, further confirming the possibility to extrapolate animal findings to humans (Buracas & Boynton, 2007; Kastner & Pinsk, 2004; Rees et al., 1997).

Taken together, the evidence on attentional modulation in these intermediate-level visual processing areas suggests that they already contribute to filtering high-level, complex information. They show preferential processing of stimuli that are momentarily important to the individual and suppress those that should be ignored. Thus, V4, IT, and MT contribute to basic visual processing and carry low-complexity information up the hierarchy, but they also participate in filtering out irrelevant information, regardless of its basic features. Overall, it seems

that attentional effects become stronger up the visual pathway, i.e., as processing gets more complex (Maunsell & Cook, 2002; Schroeder, 2001; Treue, 2001). Neuroimaging experiments have brought nuance to this view (Dugué et al., 2020; Harter & Aine, 1984; Schroeder et al., 1995). These results suggest that attention is selective enough to target certain specific levels of the visual hierarchy, depending on the task and its parameters.

Not only does attention have measurable behavioral effects, but it also modulates neuronal processes in low- and intermediate-level perceptual areas. In the nonhuman primate brain, attentional modulation can be found at every stage in the visual processing hierarchy, from the first sensory relay in the thalamus to object and motion-processing areas of the neocortex. Non-invasive neuroimaging in humans has extended this as far back as the retina itself, and has enabled a full characterization of attentional effects in V1. Kastner and Pinsk (2004) make a distinction between early (LGN to V2) and intermediate (V4 and IT) visual processing: attention in the thalamus and early visual cortex seems to increase the basic visual signal-to-noise ratio, whereas attentional modulation in the intermediate visual areas seems to enhance targets and suppress distractors. The modulation of visual areas by attention is likely the cause of its associated behavioral perceptual effects.

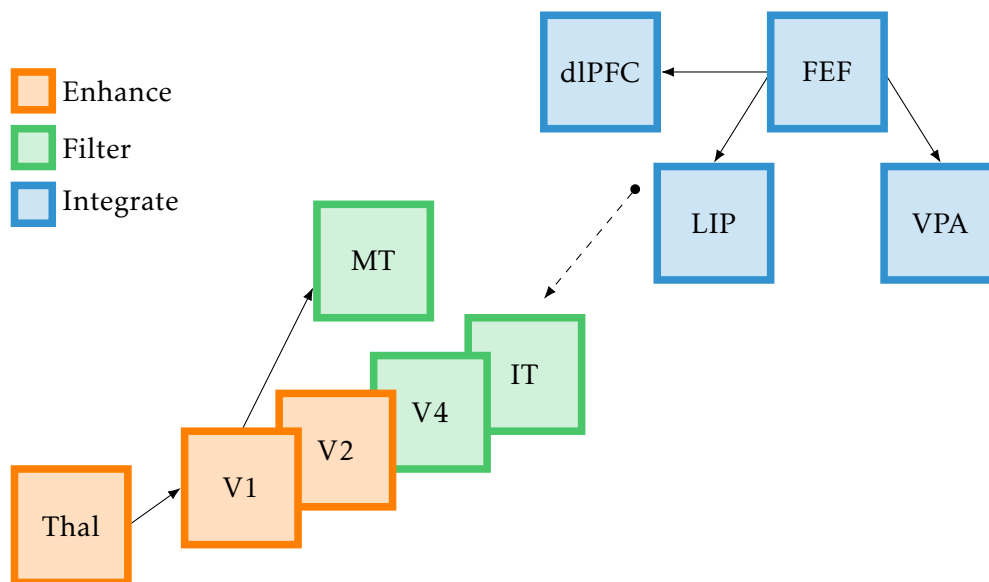


Figure I.2.7: Simplified view of the neural architecture of visual attention. Thal: thalamus, including the lateral geniculate and thalamic reticular nuclei. V1: Primary visual cortex. IT: inferotemporal cortex. MT: middle temporal cortex. SC: superior colliculus. LIP: lateral intraparietal area. VPA: ventral prearcuate area. dlPFC: dorsolateral prefrontal cortex. FEF: frontal eye field. The dashed arrow represents overall feedback from frontal to posterior regions.

2.2.3 High-level processing: a specialized attentional network

Attention transcends sensory modalities and thus constitutes a separate cognitive entity. We could, therefore, expect that it also constitutes a neural entity of its own. Moreover, sensory area neurons show differential modulation according to attentional allocation; this implies that some other physical elements (likely other neurons) are projecting onto the former and either exciting or inhibiting them. Where do these attentional projections originate?

The primate fronto-parietal network The lateral intraparietal (LIP) area is located inside a parietal sulcus, near the occipital-parietal border. Like occipital areas, its receptive fields show selectivity to simple stimuli, such as spots of light. However, gaze angle (i.e., the combination of head and eye position) strongly modulates their tuning curve amplitude (Andersen et al., 1990b). In earlier visual areas, tuning curves are usually strictly retinotopic, making LIP and other such "spatiotopic" areas highly advanced in complexity (Salinas & Sejnowski, 2010).

LIP strongly interconnects with the frontal eye field (FEF) of the frontal cortex (Andersen et al., 1990a; Kusunoki et al., 2000). LIP and FEF were originally thought to be involved primarily in the motor planning of saccades (Colby et al., 1996; Robinson & Fuchs, 1969) but several studies have shown that a dominant portion of LIP and FEF neurons encode salient visual cues instead (Bisley & Goldberg, 2003; Foley et al., 2017; Goldman-Rakic, 1988; Kusunoki et al., 2000; Powell & Goldberg, 2000; Rizzolatti et al., 1987). Attention is reflected in LIP and FEF, as demonstrated using cueing paradigms (Gottlieb and Goldberg, 1999; Robinson et al., 1995; for review see Paneri and Gregoriou, 2017), visual search (Buschman and Miller, 2007, 2009; Gottlieb et al., 1998; Mirpour et al., 2009; Sato and Schall, 2003; Suzuki and Gottlieb, 2013; Thompson et al., 1997, 1996; for review see Bisley and Mirpour, 2019), and novel attentional manipulations (Gregoriou et al., 2009; Moore and Fallah, 2001; Saalman et al., 2007; for review see Corbetta and Shulman, 2002). Moreover, studies employing simultaneous recordings in separate areas (Lennert & Martinez-Trujillo, 2013; Monosov et al., 2010; Saalman et al., 2007; Zhou & Desimone, 2011), stimulation (Moore & Armstrong, 2003), cortical cooling (Fuster et al., 1985), and lesion correlates (Barceló et al., 2000) suggest that FEF and LIP control visual areas.

A classic visual search paradigm demonstrated that the dorsolateral prefrontal cortex (dlPFC) was recruited before LIP during a difficult search, whereas LIP neurons were recruited first in easy, pop-out trials (Buschman & Miller, 2007). The dlPFC also codes for the location of covert attention (Lebedev et al., 2004). Overall, the dlPFC suppresses distractors more robustly than LIP (Everling et al., 2002; Suzuki & Gottlieb, 2013). These results support the hypothesis that top-down attentional control is exerted by the frontal cortex and saliency mapping resides in the parietal lobe.

Furthermore, the FEF becomes activated before the dlPFC, perhaps indicating that FEF controls both LIP and dlPFC in top-down attentional feedback (Buschman & Miller, 2007; Clark et al., 2015). Additional single-neuron recordings during visual search suggest that FEF uses information encoded in LIP about item saliency and identity to make the final decision on the direction of the next saccade (Buschman & Miller, 2009; Glaser et al., 2020; Mirpour & Bisley, 2021). Finally, rhesus and macaque monkey anatomical studies (Barbas, 1988; Barbas & Pandya, 1989; Ungerleider et al., 1989; Webster et al., 1994; Yeterian et al., 2012) also provide convincing evidence for the placement of FEF at the apex of the attentional top-down processing hierarchy.

Bichot et al. (2015) recently uncovered another strong candidate for the locus of a feature-based priority map: the ventral prearcuate (VPA), a region located directly anterior to FEF in the prefrontal cortex. Only little experimentation has tested the involvement of this area in attentional control (Ghadooshahy, 2017; Moore & Zirnsak, 2015; Xie & Zhang, 2020), but the anatomical separation of this area from the rest of the prefrontal cortex (Gerbella et al., 2007, 2010) supports a distinct functional role for VPA. Combined with Bichot et al. (2015)'s carefully-controlled inactivation of the VPA, including comparisons between a detection-only task, spatial attention, and feature-focused attention, these data constitute sufficient evidence to consider adding this structure as an integral part of the attentional network in the primate brain, along with the much-studied LIP, dlPFC, and FEF.

We have mentioned the importance of measuring population dynamics as well as individual neurons. Buschman and Miller (2009) followed this logic and recorded local field potentials (LFPs) in the FEF simultaneously with single cells. They demonstrated that the attentional focal point of the animal could be best decrypted from the phase of the ongoing population activity wave, i.e., *when* the neuron fired relative to the global LFP fluctuation. In a previous study, the

same authors showed that synchrony between frontal and parietal poles is significant during visual search and resides in higher frequencies during pop-out trials than during conjunction ones (Buschman & Miller, 2007). This last observation suggests that feedforward projection (sending salient information directly up the hierarchy) involves high-frequency oscillations, whereas cortical feedback (when endogenous attention is needed to control processing among the various search items) would recruit low-frequency rhythms.

LIP, dlPFC, and FEF in humans The role of the FEF and LIP as core attentional regions has largely been confirmed in human neuroimaging studies (for review see Kanwisher & Wojciulik, 2000). FEF and LIP are also strongly activated during attentional anticipation in humans (Beck & Kastner, 2009) and analyses of fMRI time series confirmed that FEF controls the intraparietal sulcus (IPS), of which the LIP is part (Bressler et al., 2008; Clark et al., 2015). These regions show attentional activation even in the absence of any visual stimulation, and more so than intermediate areas (Kastner et al., 1999). The dlPFC was also found to be selectively activated in human participants during attentional focus (Casey et al., 2000). Neuroimaging methods further allowed the uncovering of attentional regions that had not been accessed in nonhuman primate recordings: these are reviewed in the next section.

2.2.4 The distinctive human attentional network

Separation by ventral and dorsal cortices We are often voluntarily focused on something, e.g., reading a long thesis. However, an important event such as a partner coming home or the ding of a coffee maker requires our attention to be moved away and captured by the new stimulus: this process is typically termed "reorientation" in the literature on human attention. Corbetta and Shulman (2002) suggest that the network for bottom-up, saliency-driven attentional reorientation (a type of *selection*) is separate from the network for top-down, ongoing, goal-directed attentional control (akin to *facilitation*). The saliency-driven network would be composed of right-hemispheric areas only: the temporoparietal junction (TPJ) and ventral frontal cortex (VFC) (Braver, 2001; Clark et al., 2000; Corbetta et al., 2000; Downar et al., 2000; Kiehl et al., 2001; Marois et al., 2000). These two saliency-driven regions are more ventral than the bilateral FEF and IPS, which would, in turn, constitute the top-down network's main elements. Additional support for this ventral-dorsal, selection-facilitation distinction comes from fMRI studies also involving the Insula, superior frontal gyrus (SFG), anterior cingulate cortex (ACC), and dlPFC (Casey et al., 2000; Coull et al., 2000) as well as the pre- and postcentral gyri, the frontal gyrus, the superior parietal lobule (SPL), and the IPS (Hopfinger et al., 2000). The right-ventral network and bilateral dorsal network were recently confirmed to constitute two separate entities in an analysis of temporal dynamics in the ventral and dorsal networks: correlations *within* each one are strong, but there is close to no relation in spontaneous fluctuations *between* them (Fox et al., 2006).

The involvement of the TPJ was recently confirmed and extended (Dugué et al., 2017a), showing that the TPJ in both hemispheres may also contribute to attentional reorientation and that the posterior subdivision of this area is active in reorientation from both exogenous and endogenous attentional capture. In contrast, the central TPJ is only involved in reorienting attention following endogenous capture. These new results suggest that the role of each attentional area in the human parietal-frontal network is more specialized than that of nonhuman primates. The human attentional network may include within-area subdivisions for the control and management of specific sub-types of attention.

Additional regions of the human attentional network The posterior parietal cortex (PPC) remains activated when a stimulus needs to be kept in focus (Curtis, 2004; Jonides et al., 1998) and shows a strong modulation during attentional orientation in space (Beck & Kastner, 2009;

Kastner & Ungerleider, 2000). These findings suggest that the PPC contributes to attentional control in humans. The superior and inferior parietal lobules (SPL and IPL) and the supplementary eye fields (SEF) are also recruited in a number of visuospatial attentional tasks (Kastner & Ungerleider, 2000; Pessoa et al., 2003), sometimes independently from visual stimulation (Kastner et al., 1999). Similarly, the postcentral sulcus (anterior to the IPS) has been reported to show consistent activation by attention (Corbetta et al., 2000; Hopfinger et al., 2000; Shulman et al., 1999), indicating that the human attentional network is more expansive than the nonhuman primate one.

In summary, the attentional modulation observed in low- and intermediate-level perceptual areas seems to originate in high-level fronto-parietal areas. From the evidence gathered so far in nonhuman primate electrophysiology and confirmed by human neuroimaging, the frontal eye fields (FEF) seems to act as an attentional orchestrator. Under this viewpoint, the FEF is at the apex of attentional modulation in the primate cortex (see Figure I.2.7). It projects to the dorsolateral prefrontal cortex (dlPFC) and lateral intraparietal area (LIP). The LIP, dlPFC, and a newly uncovered region named the ventral prearcuate (VPA) exhibit saliency-map-like properties. They project back further to intermediate-level visual regions MT, IT, and V4. The attentional network in humans recruits the same areas as the nonhuman primate one and additional structures, perhaps indicating that human attentional functions are more complex and require the contribution of a more extensive network. Finally, we have seen that periodic fluctuations in neural activity seem to play an important role in attentional coordination between brain areas. High-level attentional areas show a clear dependence on temporal synchrony, possibly reflecting the periodic sampling observed in behavioral studies of attention. The perceptual and attentional cortical networks are of high complexity, as made evident by the somewhat disparate collection of results shown here. What attempts have been made to unify these processes and explain their mutual relations?

2.3 Computational modeling of attention's neural underpinnings

2.3.1 What is a computational model?

As we have seen with cognitive modeling, theoretical simulations constitute a powerful tool for understanding how the world functions. This, of course, extends to brain mechanisms, for which the simulations are typically termed *computational models* (see Figure I.2.8). Computational models typically see neuronal processes as mathematical operations and rest on biological evidence to interpret and build a picture of how the brain deals with information. To cite one example which we have introduced, fitting Gaussian functions to neuronal tuning data (see Figure I.2.4) has enabled neuroscientists to mathematically describe the relation of the neuron to the external world and the modulatory influence of neurons onto one another. Importantly, Gaussian fitting quantifies how neural systems may optimize processing through simplified mathematical relations (for more details, see Salinas & Sejnowski, 2010).

The first general step in computational modeling is to build the model itself. It usually entails gathering anatomical and functional data about the system (in our case, the brain) and emitting hypotheses about which mechanisms may produce such data. These mechanisms are implemented to form a simulation of the hypothesized neural process. Originally these simulations were almost entirely mathematical and theoretical, but today most are computerized. Thus, in modern computational modeling, two essential tools are used to create a simulation: mathematics and programming. Mathematical functions and relations are fit to the observed

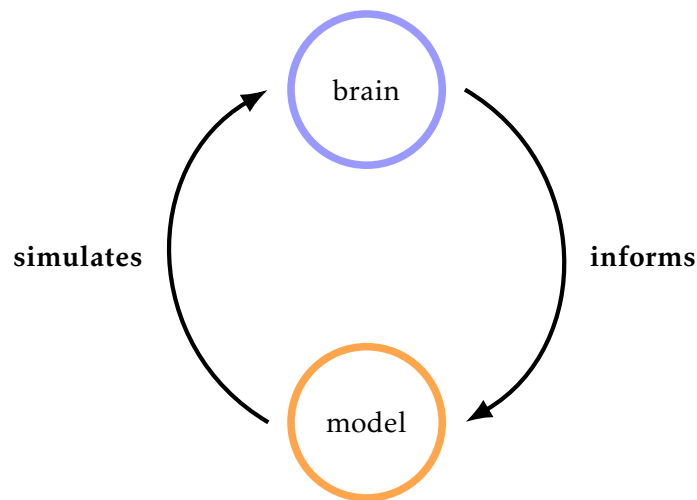


Figure I.2.8: The virtuous cycle of computational modeling. The brain informs the model, which is made more and more reflective of the brain, and the model simulates the brain, yielding useful predictions, making measurements constantly more precise and consistent.

data in an attempt to describe the underlying process as simply and as accurately as possible. With the wide availability of high-performance computers, it is now possible to implement the defined mathematical relations into digital simulations, augment them with computer abilities such as logical assignment and looping, and predict outputs with a high resolution. Thanks to our digital simulation, we are capable of predicting events and signals with high precision. Thus, a comparison is possible between the model's predictions and empirically measured signals. We are able not only to test whether the model accurately represents neural mechanisms but also to adapt and refine our simulation parameters to best match the measured data.

By definition, theoretical modeling implies "filling in the gaps" for the components we cannot measure directly. Therefore, the simulations will never reflect reality in its finest details, unless we are hit with exceptional strokes of luck. However, the goal of computational modeling is not to simulate reality exactly. Instead, it aims to guide our understanding of the brain and yield useful predictions and applications for future testing. Models reveal how complex processes *can* and *cannot* work, in terms of logic, mathematics and computation. In the case of cognitive neuroscience, they constitute a major tool to link neurophysiology and behavioral measures. Ideal computational models simulate the nervous system with an appropriate level of detail to yield useful, testable predictions of both the neural system and the organism's behavior which can then be tested with recording techniques and psychological measures, respectively (Wilson, 1999).

2.3.2 Models of attention

Cognitive resources are limited (Lennie, 2003). One key goal in neuroscientific computational modeling is to describe how the brain can implement cognitive processes at a minimal energetic cost. If attention can be considered as a set of strategies to minimize the computational load of visual perception (Tsotsos & Rothenstein, 2011), it constitutes a function of high interest for computational modeling.

Some important distinctions must be made between the different attentional processes that are (or seem to be) taking place in the brain. One such distinction is the difference between attentional *selection* and *facilitation*. As we have seen, when two stimuli are presented inside the same receptive field of a visual neuron, e.g., a V4 cell, the response is driven by the attended stimulus, and the response that would be observed if the unattended stimulus were presented

alone is suppressed (Luck et al., 1997; Moran & Desimone, 1985; Reynolds et al., 1999). This has been categorized as a result of attentional *selection*, as one stimulus is effectively selected within the receptive field, and the other is discarded. These results support the overarching view of attention as a selection process, giving an advantage to certain specific stimuli and ignoring others.

Another key result is that one single stimulus will elicit a stronger response if it falls at a location that is presently attended, compared to presenting the same stimulus while the location is not attended (Connor et al., 1997; McAdams & Maunsell, 1999). This latter result is termed *facilitation* because there is no competition between stimuli, simply the overall enhancement of processing in the presence of attention. Another way to separate these results might have been to call selection "feature-based" or "object-based" attention, as it is akin to discriminating features at a single spatial location, and facilitation "spatial attention" since the important variable is the locus of attention, and features were not considered. However, attentional *facilitation* has also been demonstrated for attended features, rather than locations (Patzwahl & Treue, 2009; Saalman et al., 2007), so we cannot equate spatial attention and facilitation.

Contrast Gain vs. Response Gain We have presented studies in which attentional *facilitation* is observed within intermediate-level visual cells (Connor et al., 1997; McAdams & Maunsell, 1999). However, other reports we have discussed do not observe facilitation, although the experimental conditions are comparable (Haenny et al., 1988; Moran & Desimone, 1985). To resolve this discrepancy, Reynolds et al. (2000) built two models that could explain the lack of facilitation in the case of stimuli presented with excessively high or low contrast. They tested their two models using a paradigm specifically designed to differentiate between a contrast gain, i.e., a gain modulation only at intermediate levels of stimulus contrast, and a response gain, which can be thought of as a multiplicative gain at every level of contrast and would result in strong response increases even at high stimulus contrast. This latter possibility does not seem theoretically plausible, as attention is more likely to aid perception when it is ambiguous; attention is not typically needed when a stimulus is very easily detected. Thus, unsurprisingly, their data favored the contrast gain model, confirming that gain modulation by attentional facilitation occurs at intermediate levels of contrast, i.e., when the stimulus is ambiguous or hard to distinguish.

This model is theoretical in the sense that it predicts response behaviors without simulating the neurons themselves, placing it somewhere at the border between cognitive and computational models, without necessarily falling into either one of these categories. Nonetheless, it has provided an instrumental account of disparate results. It has been very influential in orienting measures of visual neurons after its publication, by informing future experiments of the range of stimuli contrast at which gain modulation should be observed.

Receptive field shifts Models of receptive field (RF) shifts have been proposed, as they can explain much of the experimental data recorded on spatial attention (Anton-Erxleben & Carasco, 2013). When two stimuli fall within the same RF, the neuronal response resembles that of the attended stimulus when presented alone (Williford & Maunsell, 2006). This attentional *selection* at the level of the neuron can be pictured as a shrinking of the neuron's receptive field around the attended stimulus only, thus excluding any others.

This process could involve only the affected RF, meaning that the visual space left around it (which it previously included) no longer falls into any cell's RF (unless the RFs were initially overlapping). It could also be achieved by nearby cells' RFs elongating in the direction of the attended stimulus to cover the space left by the shrinking one. In this scenario, we should see the distractor stimuli appear in neighboring cells' receptive fields. As we have introduced, this is exactly what neurophysiological RF maps show, at different levels of the visual hierarchy (V4: Connor et al., 1996, 1997; MT: Anton-Erxleben et al., 2009; Niebergall et al., 2011; Womelsdorf

et al., 2006; LIP: Ben Hamed et al., 2002; for reviews see Anton-Erxleben and Carrasco, 2013; Treue, 2014). How might neural processes manage this feat?

Both the biased competition model (Compte & Wang, 2006) and feedback models (Miconi & VanRullen, 2016) can account for RF shifts (see their dedicated sections below). As we have seen from behavioral studies, spatial resolution seems to be improved at the attended location (Anton-Erxleben & Carrasco, 2013, for review see). Moreover, resolution at unattended locations is worsened (Montagna et al., 2009). These results could be explained by RFs shrinking at the attended location and becoming inflated on the rest of the visual field, allowing for finer spatial processing at the attentional locus and degrading it elsewhere. If this were the case, we would see a warping of the RFs over the whole visual space, not only around the focus of attention. Indeed, the strongest argument favoring RF shifts seems to be the central performance drop (CPD) in texture segmentation tasks and its associated performance-over-eccentricity curve. In the case of textures exhibiting intermediate spatial frequency, texture segmentation performance peaks in the near periphery (Yeshurun & Carrasco, 1998). However, when attention is allocated to the location of the texture target, the peak shifts outward (Talgar & Carrasco, 2002), suggesting that attention increases the resolution in the periphery. This finding is consistent with RF shrinking. However, the effects reported could also be explained by an enhancement of high spatial frequency filters over low ones when attention is allocated to the texture location (Carrasco et al., 2006; Yeshurun & Carrasco, 2000).

The RF shifting model has been debated (Tsotsos & Rothenstein, 2011, see below), as some results taken to support it may be explained by feature-based attentional modulations (Treue, 2014). Others necessarily imply feature modulation, e.g., when the two stimuli (attended and unattended) are strictly overlapping (Patzwahl & Treue, 2009). In that case, a receptive field shift could not aid (nor impair) the processing of one stimulus over the other.

Selective Tuning As neurophysiological evidence of the cerebral effects of attention accumulated and precise measures of attentional *selection* were obtained, it became evident that attention not only selects important stimuli or regions but also needs to suppress irrelevant ones (Chelazzi et al., 1993; Luck et al., 1993, 1997). The field found a growing need to account for this bipartite function of attention as revealed by neural recordings. Selective tuning provided such an account by proposing a view of attention as a *filtering* operation. According to Tsotsos and Rothenstein (2011), selective tuning is not like other theories in the sense that it does not try to explain past results. Instead, it uses known biological mechanisms to predict how cognition will operate. With Desimone and Duncan (1995)'s biased competition model (see below), these studies set the standard to move away from rather "psychiatric" mind models (in the sense that they are not biology-based) towards using what we know about the physical brain in order to understand psychological effects down the line.

The selective tuning model rests on a "hierarchical processing pyramid" (Tsotsos & Rothenstein, 2011, p.19) with both feedforward and feedback connections, the former being in charge of pushing stimulus information up the hierarchy and the latter exerting attention control from the top of the pyramid downwards. Once all stimuli reach the higher levels, attention would apply a first filter and inhibit processing of irrelevant items through feedback ("winner-take-all"), thus reducing interference within the large receptive fields at high levels of visual processing. There is no need for receptive field shrinking in this model.

The selective tuning model received substantial empirical support after its implementation. We have seen in Section 2.2.2 on attentional modulation in the primate cortex that attentional *filtering* is reflected in neuronal response modulation in intermediate- and high-level areas, where many-to-one mapping occurs, and that higher-level areas are typically modulated by attention first, followed by intermediate- and lower-level ones (Britten, 1996; Cutzu & Tsotsos, 2003; Kastner et al., 1998; Mehta et al., 2000a; Reynolds et al., 1999; Vanduffel et al., 2000).

Psychophysical tasks have been instrumental in researching the properties of sensory per-

ception and to guide knowledge about its neural underpinnings. In one example among many, Cutzu and Tsotsos (2003) performed psychophysical experiments to test the predictions of their neuronal theory of selective tuning. Purely behavioral tasks permitted them to map the attentional field of participants and verify the validity of a specific neuronal mechanism. They used a cueing procedure to focus participants' attention at one pre-determined location, and probed perceptual performance at various locations around the cued one to map the attentional field. They found that participants' performance on a shape discrimination task is significantly reduced in a short radius around the cued location. Surprisingly, performance increases again at further locations. This effect corresponded to the prediction made by the selective tuning model and was confirmed in other behavioral studies using psychophysics (Bahcall & Kowler, 1999; Caputo & Guerra, 1998).

Biased Competition During attentional *selection* among stimuli, one item is selected and the others discarded. There seems to be an inherent competition for processing by intermediate-level visual cells when multiple items are close enough to fall within a single RF. How might this competition be implemented in visual cortical areas? Desimone and Duncan (1995), Duncan (1998), and Reynolds et al. (1999) attempted to answer this question with their biased competition (BC) model. The BC model proposes a mechanism of neural activity and connectivity which has successfully reproduced these results.

Any stimulus can be temporarily considered relevant even if it holds no intrinsic value to the observer (for example, a simple square might become important if it is the target of a visual search). The perceptual system thus needs to create a template of what is currently important. The BC model proposes that competition between units in the visual system is biased towards this template. Therefore, when the distractors are very different from the template, they receive almost no competitive advantage, and the search is easy. Conversely, when distractors are hard to discriminate from the template, they receive positive bias. In that case, the competition is more "equal," and the search is difficult.

Neurally speaking, the units are simulated as a high and a low layer of neurons, with low neurons projecting to higher ones via both excitatory and inhibitory connections. Only feedforward connections are taken into account. Thus, no "higher" attentional area exerts any control back onto lower ones. This organization entails that attention emerges on the dynamics of the visual system itself (Tsotsos & Rothenstein, 2011). The lower neurons correspond roughly to the cells found in V1, with small RFs and more specific selectivity, while the higher units may correspond to V4 cells, with larger RFs and less specific tuning. Attention would strengthen the signal of those lower cells corresponding to the attended stimulus, by multiplying the weights of their (excitatory and inhibitory) connections to the higher cell (Reynolds et al., 1999). Feature integration theory (FIT) and other two-stage models presented above typically include a step of serial processing (Treisman & Gelade, 1980). In the BC model, there is no serial component: all items are processed in parallel and compete for neural resources simultaneously.

This model enabled the field to move away from the debate between "early" and "late" attentional processing (Broadbent, 1957; Shiffrin & Schneider, 1977), and showed that it is computationally possible for attention to be recruited at different levels of the sensory hierarchy depending on stimulus properties and the task at hand (Spratling & Johnson, 2004). Crucially, it proved that even with only feedforward connections from low to high sensory areas, task demands and attentional load alter neural processing and yield different predictions of neural signals and behavioral performance. Similarly, a separate feedforward-only model accounts for neuronal selectivity (Priebe & Ferster, 2008). Up until then, the spatial and feature selectivity of neurons (the tuning curves of neuronal responses to different dimensions, such as location in the visual field, bar orientation, or motion direction) could only be accounted for by models which included lateral inhibitory connections between neurons in the same area. However, these lateral inhibitions have not received convincing support from electrophysiology (Priebe

& Ferster, 2008). Thus, like the BC model, Priebe and Ferster (2008)'s model only includes feedforward connections but still reproduces visual properties which until then were thought to require lateral inhibitory connections.

Feature similarity gain The biased competition model mainly focused on spatial attention results, although it could also explain some feature- or object-based attention findings. Martinez-Trujillo and Treue (2004) proposed another account for results found in the middle temporal (MT) area that removed the spatial component and which did not verify the predictions of the biased competition model.

Overlapping random dot patterns moving in opposite directions were placed at a single location in the visual field, and the animals were trained to attend to one direction only (Treue & Martinez-Trujillo, 1999). In that case, both the attended and unattended stimulus subtended the same visual space, so a receptive field shrinking could not account for attentional facilitation. Moreover, there was no response suppression from distractor presence, which is usually interpreted as a marker of competition between stimuli. Unlike competition models, in which attention affects the contest for neural representation between visual stimuli, the feature similarity gain model assigns modulatory power over whole populations of neurons to attention. The modulation is seen as independent of the visual stimuli: attention multiplicatively modulates the gain of responses without changing the shape of the tuning curve (Treue, 2014; Treue & Martinez-Trujillo, 1999). This model includes feedback projections and is the first account for gain modulation in the neural system (Tsotsos & Rothenstein, 2011).

Feedback models Feedback connections play an important role in the visual system and especially in the attentional processing of information, but the models we have presented so far did not include top-down projections. Spratling and Johnson (2004) extended the biased competition model of attention and created a biologically-inspired neural network that simulates the cortex with feedback connections, and the results match physiological data. It can also explain figure-ground segregation and other top-down processes such as feature binding, disambiguation, and contextual cueing (showing the same local stimulus within different visual contexts). It functions by defining the dendritic arbor of pyramidal neurons as one large dendrite with two "branches" (apical and basal). The basal dendrite integrates feedforward inputs (coming from lower areas). In contrast, the apical dendrite integrates feedback information (signals from higher processing levels). The result of the apical integration modulates the output of the basal dendrite. In turn, this output has two targets; in reality, two outputs would come from two separate pyramidal neurons in two separate layers, but they seem to perform similar computations within a cortical column, so they are modeled as one unit. One output projects to the apical dendrites of lower-level regions (feedback), and the other projects to the basal dendrites of higher-level regions (feedforward). Neurons within one region also compete via lateral inhibition onto each other's basal dendrites, so the basal dendrite integrates signals coming from lower areas and from its neighbors. In this feedback model, higher-level areas are assigned weights at specific spatial locations or for particular features "by hand" (by the experimenters), meaning that in the physical brain, they would need to be set by external, "attentional" areas.

Because it can account for results previously considered disparate and unify various representations of attentional and even non-attentional processes (e.g., familiarity), this model suggests that the general mechanism of feedback projection serves as the overarching functional implementation of higher-level cognition in the visual system. Hamker and Zirnsak (2006) showed that feedback models can further explain high-speed object recognition, potentially without attention, and are compatible with previous models and results supporting receptive field shifts controlled by attention (Desimone & Duncan, 1995; McAdams & Maunsell, 1999; Moran & Desimone, 1985; Reynolds et al., 1999). Hamker and Zirnsak (2006) applied the bases

of the feedback model to include higher-level areas: inferotemporal cortex (IT), two sub-regions of the frontal eye field (FEF), and the intermediate visual processing area V4. Their feedback model application reproduced electrophysiological results discussed previously and provided them with a potential explanatory mechanism. More recently, Miconi and VanRullen (2016) revisited the feedback model and showed that top-down modulation of intermediate areas (e.g., V4 and middle temporal cortex, MT) combined with lateral competition suffice to modulate neural responses, resize and shift receptive fields, and reproduce effects of inhibition between neighboring cells.

Inhibition of return Items that have previously been fixated during a search show weakened LIP activation, thus marking them as non-targets and preventing new saccades to already identified items (Gottlieb et al., 1998; Mirpour et al., 2009). One plausible explanation for this finding is inhibition of return, i.e., a mechanism that prevents searching the same location or feature twice. Building biologically plausible models accounting for the phenomenon of inhibition of return is complicated because recordings are relatively scarce, resulting in a poor understanding of the underlying neural mechanisms (Klein, 2000). Thus, the models that attempt to describe its possible implementation are generally based on engineering solutions rather than biological systems (Tsotsos & Rothenstein, 2011). The same is true of object recognition. It is difficult for computational neuroscientists to model the fate of selected and non-selected items because there is a lack of knowledge about the high level structures that would use such information. These processes might lean towards less-studied functions, like consciousness. Two models are of note, however, because they integrate many attentional and decisional mechanisms, including inhibition of return and saccadic remapping, thus proposing a more comprehensive account of moment-to-moment and interareal attentional processing (Lanyon & Denham, 2004; Zaharescu et al., 2005).

Normalization models Normalization models were first implemented in the 1990s (Albrecht & Geisler, 1991; Heeger, 1991) and further established by Reynolds and Heeger (2009). Their founding principle is that neuronal responses are normalized (divided) by a "common factor," which is calculated from the sum of the input activity of the neuron pool (and a free constant that determines the shape or saturation; for details, see Carandini and Heeger, 2012). They do not propose a physical implementation for the normalization process, only the computations themselves. Other groups have proposed this type of "quantitative" model of attention, with the common trait that a systematic response normalization determines attentional effects (Boynton, 2009; Ghose and Maunsell, 2008; Ghose, 2009; Lee and Maunsell, 2009, 2010; for review see Treue, 2014). They are seen as mathematical support for the biased competition and feature similarity gain models.

A recent paper applied the normalization model to temporal attention, with the intent to "formalize and generalize the idea of limited attentional resources across *space* at a single *moment*, to limited resources across *time* at a single *location*" (Denison et al., 2021, emphasis added). The model simulations successfully reproduce many of the results we have presented, especially in recreating multiplicative gain modulation. The normalization model has been found to account for results in many other, non-attentional cognitive operations and modalities outside of visual sensation, making it, like gain modulation (Salinas & Sejnowski, 2010), a possible overarching mechanism of neural functioning (Carandini & Heeger, 2012).

Computational models of visual search The cognitive models of visual search presented above (Section 1.3.2) have since been extended to include computational principles and neural recording predictions. We will examine these specific models in Chapter II.

2.3.3 Modeling cortical temporal dynamics

Amplification of signals through synchrony Another approach to explaining how neuronal tuning curves may show non-linear (multiplicative) gain modulation is through alteration of synchrony (Fries et al., 2001; Salinas & Sejnowski, 2010; Salinas & Sejnowski, 2000; Steinmetz et al., 2000). As we have seen, part of certain neuronal signals seems to depend on their temporal relationship with the global response of the population (see, e.g., Saalmann et al., 2007). Indeed, synchronization between neurons is enhanced during attentional focus, and this modulation has been shown to affect not only the neural behavior but also, at the macroscopic level, the individual's behavior (Fries et al., 2001; Treue, 2014; Womelsdorf et al., 2006).

Fries et al. (2001) used spike-triggered averages to measure oscillatory synchronization in V4. They recorded the spiking activity of a single neuron while simultaneously recording the local field potential (LFP) from another locus within the same area (far enough to avoid any contribution by the single neuron to the LFP measured at the other electrode). They marked the spikes from the single neuron, plotted the LFP over a time window spanning from just before to just after the spike (-150 to +150 ms), and averaged these windowed, spike-locked LFPs together. If the timing of the single-neuron spike relative to the population LFP has any importance, the average LFP should form a visible wave around the spike, revealing the phase at which the spiking occurred the most. If not, the average of peri-spike LFP should be flat. Not only was a phase relationship evident, but the authors also found that neuron spiking and LFPs would synchronize more strongly when monkeys attended inside the single cell's receptive field, compared to when they attended elsewhere. Thus, synchronization of activity seems to be a natural property of the cortex, and it is modulated by attention.

In another study, increased synchrony was observed while the animal was attending to a feature held by the stimulus inside the RF, versus lower synchrony when the same stimulus did not possess a searched feature (Bichot et al., 2005). This result shows that synchrony is at play not only in spatial but also in feature-based attention. Fries et al. (2001) explained that "modulating synchronization at precise locations in the cortex might be a fundamental neuronal mechanism for amplifying signals that represent behaviorally relevant stimuli" (p.1563). A large body of evidence now supports the theory of periodic synchrony reflecting spatial and feature-based attention in the neural substrates supporting perception and attention (Gregoriou et al., 2015; Paneri & Gregoriou, 2017).

Synchrony at a small scale, between neurons and neuronal populations, is modulated by attention and only increases in those neurons processing a relevant stimulus (Fries et al., 2001). This may be explained in terms of synaptic input: a regular temporal "packaging" of spiking in the form of oscillations enables neurons to provide input simultaneously to their targets. Simultaneous activity may enhance the signal, for a multiplied input will have a much more significant impact on downstream neurons than the same number of projections happening asynchronously (Fries, 2005; Paneri & Gregoriou, 2017; Salinas & Sejnowski, 2000, 2001).

At the next level of scale, i.e., concerning synchrony between cortical areas, evidence from optogenetic rhythmic manipulation combined with a computational model suggests that efficient communication between areas involves matching the temporal dynamics of the output area to the timing of inhibition in the target area, in order to fall into a favorable "window of excitation" (Cardin et al., 2009; Knoblich et al., 2010). Stimulation of V1 neurons elicited gamma LFP activity in V4, and stimulation of V4 neurons evoked low-frequency (5-15 Hz) activity in V1 (van Kerkoerle et al., 2014), further supporting the idea that high-frequency gamma (40-90 Hz) fluctuations orchestrate feedforward input whereas low-frequency theta/alpha/beta rhythms (5-30 Hz) coordinate feedback projection (Clark et al., 2015; Wang, 2010). Furthermore, deep neocortex layers (5/6) tend to exhibit beta oscillations (and theta in anesthetized rats; Wang, 2010). Thus, beta oscillations' power may reflect top-down feedback from "higher" areas to "lower" (cortical and subcortical) areas.

What synchrony can teach us What we know of the neural underpinnings of attention in healthy humans largely relies on oscillations. Several studies from the neurophysiology and neuroimaging literature rely on Granger causality, which uses time series and their characteristics to calculate if one signal can be better predicted when taking a second signal into account (Bressler et al., 2008). van Kerkoerle et al. (2014) used this method to compare the LFP time series of visual regions in nonhuman primate brains. After Bressler et al. (2008)'s use of this powerful tool in the BOLD time series, it has become increasingly used, particularly in EEG and MEG studies in which temporal resolution is extremely high.

Using MEG, Jokisch and Jensen (2007) found that alpha power (8-12 Hz) increases in the dorsal stream of visual processing (the "where" pathway) when the ventral stream is needed (the "what" pathway). Conversely, alpha power decreases in the dorsal stream while participants perform a spatial task (recruiting the ventral stream). The most parsimonious interpretation of this dichotomy is that alpha power reflects functional inhibition at the level of neuron populations. Many findings of alpha lateralization during visual attention support this view: alpha power becomes suppressed in the occipital hemisphere corresponding to the site being attended, and strong alpha power arises in the unattended one (Fu et al., 2001; Kelly et al., 2006; Sauseng et al., 2005a; Thut et al., 2006; Worden et al., 2000; Yamagishi et al., 2005). The inhibitory power of alpha oscillations was further confirmed with simultaneous single-neuron and LFP recordings (Haegens et al., 2011).

The following section will present a more detailed account of temporal synchronization in the human cortex and its behavioral implications. We will examine how the link between scalp-recorded oscillations and behavior supports a strong role of oscillatory activity in neural functioning and cognition.

In short, computational neuroscientists have successfully filled many gaps in the sparse information provided by the electrophysiological recordings presented throughout this section. Computational models have tied together the different clues concerning the neural implementation of perception and attention gathered over time. Notably, temporal synchrony appears to play an essential role in orchestrating neuronal processes, as described by models of periodicity in neuron relations. This synchrony at the microscopic level may reflect the periodic sampling observed at the behavioral level. Thus, models of neuronal synchrony constitute further support for the theory of temporally discrete perceptual and attentional sampling. The next section will present a more detailed account of temporal synchronization in scalp-recorded signals and its behavioral implications.

3 Oscillations: a tool to study attention as a cognitive and neural process non-invasively

As we have seen, neuronal response and transmission may be amplified by synchrony. When researchers began to take an interest in the oscillations emanating from the brain, a popular idea was that each frequency or frequency band reflected a distinct neural process and must be associated with a single cognitive function. When taken separately, many clues point to this conclusion. However, the relationships between oscillatory frequencies and cognitive processes may be more complex than was described initially. This topic will be covered in detail in

Chapters II and III; we only provide a brief introduction here.

When gamma power disappears and delta and theta power increase significantly in the mouse cerebrum after genetic manipulations, the animals no longer exhibit normal cognitive functioning. They lose consciousness and manifest sleep troubles. The oscillatory changes may be side-effects of the cellular manipulation, but it remains the case that sufficient gamma power and moderate low-frequency amplitude seem necessarily present during normal cognitive functioning (Llinas et al., 2007). Certain oscillatory characteristics also correlate with normal psychological functioning in humans. Ferrarelli et al. (2008) found that schizophrenic patients' prefrontal cortices showed a reduced-amplitude oscillatory response to cortical stimulation, compared to neurotypical individuals. A plethora of studies have shown impaired neural connectivity in schizophrenia and associated symptoms (Garrity et al., 2007; Hoffman & McGlashan, 1998; Lawrie et al., 2002; Liu et al., 2008; Williamson, 2007), resulting in different oscillatory profiles than those found in neurotypical controls (Friston, 1999; Uhlhaas et al., 2008; Uhlhaas & Singer, 2010). Abnormal oscillatory structure has also been found in Tourette's syndrome (Leckman et al., 2006), Alzheimer's disease (He et al., 2009), autism (Wilson et al., 2007), and other psychiatric profiles (He et al., 2007; Uhlhaas, 2009; Uhlhaas & Singer, 2006; Wilson et al., 2008). These results indicate that oscillations are an integral part of neurological functioning and can as a marker for cognition.

3.1 Additive evoked activity vs. phase reset

The waveforms observed in evoked response potentials (ERPs) result from averaging all of the trials' individual signals together. Sauseng et al. (2007) showed that we cannot, therefore, differentiate between two possibilities: an additive amplitude component or a phase reset (see Figure I.3.1 for an illustration). The former results from a "piece of signal" with fixed amplitude getting summed onto each trial after stimulus onset, regardless of its initial state. Because the initial state can vary from trial to trial, its average is flat, and only the additive component remains evident in the ERP. This first possibility is the classic interpretation of ERP activity. However, the same response profile can be achieved through a phase reset, in which the ongoing signal shifts to the same instantaneous phase relative to stimulus onset at every trial, resulting in the signal from that time point onward looking very similar from trial to trial and thus appearing in the averaged signal.

Therefore, ERPs confound amplitude and phase effects because averaging the recorded signals yields the same result for a strong-amplitude, weakly phase-locked potential, and a low-amplitude, strongly phase-locked one (Cohen, 2014). We have mentioned that the first findings in EEG research reported oscillatory effects, whereas investigation using ERPs exploded after the first evoked potential reports in the 1910s. Decomposing oscillatory signals is a computationally heavy process and may have been too complex and inaccessible before the computer era. With access to appropriate tools, we can now better understand the oscillations measured from the scalp and use them to relate brain processes to cognitive functioning. Rizzuto et al. (2003) showed that low-frequency (7-16 Hz) neural oscillations' phase significantly impacts working memory, which attentional tasks typically call upon, and that a phase reset of ongoing oscillations explains the results. Evidence suggests that other classic components of ERPs may be explained by phase resetting (Sauseng et al., 2007).

In contrast, Shah et al. (2004) measured LFPs during visual stimulation and reported that primary visual cortex (V1) activation affected the amplitude, rather than the phase, of LFP activity. They reasoned that the large waveform resulting from averaged signals could not be due to a phase reset because the spontaneous LFP activity in V1 had a very low amplitude.

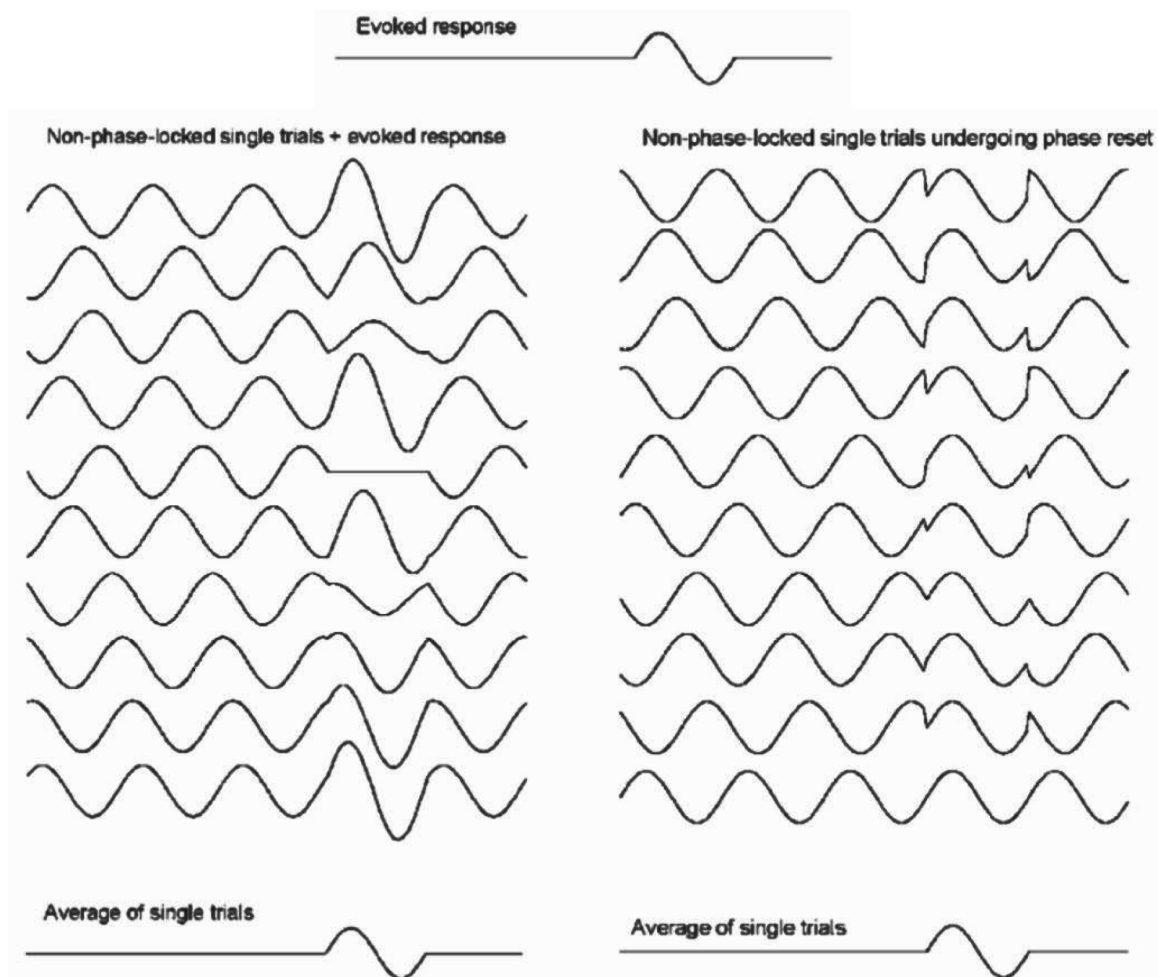


Figure I.3.1: Possible contributions to the evoked response potential (ERP). The ERP may reflect an additive amplitude component (left) or a phase reset (right). Adapted from Sauseng et al. (2007).

These disparate results illustrate the utility of decomposing the signal into amplitude and phase so that we may know whether the averaged response is due to an additive evoked response (affecting amplitude) or a phase resetting (affecting phase-locking). Oscillatory power seems to reflect synchronized firing of neuron masses in the form of large simultaneous inputs to cells (post-synaptic potentials), which are mainly recorded from the dendrites of pyramidal cells (Nunez & Srinivasan, 2006). Recent measures of oscillatory phase have revealed that this wave property is also highly informative. We have seen that in mammalian hippocampal place cells, the phase of the ongoing wave codes for the animal's direction of motion (O'Keefe & Recce, 1993). The phase of a first oscillation in one frequency can directly relate to the amplitude in another, suggesting that the first controls the second via its phase (Fiebelkorn & Kastner, 2019).

A recent study (Zazio et al., 2021) aimed to clarify the difference between pre-stimulus power and phase effects in visual detection. It suggests that power and phase reflect separate phenomena, because they originate from different brain areas: power is localized in contralateral occipital-temporal lobes, whereas phase also recruits ipsilateral regions of the prefrontal cortex. Only power differences affected detection performance in the post-stimulus period: post-stimulus phase did not correlate with behavior in this paradigm. Indeed, as we have seen above, phase resetting seems to reflect high-level attentional processes, whereas low-complexity perceptual processing, such as in this detection task, seems to affect amplitude.

Thus, we can tell the difference between phase and amplitude effects by analyzing neural

oscillations (i.e., decomposing cortical signals by oscillatory characteristics). This possibility opens the way to substantially more informative measures of the neural system. By decomposing the signals into more basic components, we can relate specific neural properties to their behavioral counterparts.

3.2 Neural oscillations reflect key neural processes

3.2.1 Synchrony may be the neuronal coordinator

EEG and MEG (sometimes referred to using the single term "MEEG") mainly reflect activity of the apical dendrites of pyramidal cells in the more superficial layers of the cortex, at a large scale. This global view gives us the right balance of precision to study temporally precise neural events while remaining at a sufficiently elevated level to relate this information directly with cognition (Nunez & Srinivasan, 2006). As hinted by LFP recordings in nonhuman primates, early EEG recordings, and the comparison between neurotypical and atypical profiles, synchrony at the level of neural populations and brain areas seems to be a fundamental property of the nervous system.

Spontaneous oscillations are always present (Buzsáki, 2006): their origin, or the mechanisms giving rise to them, remain the topic of debate, but research has given rise to some explanations. Computational models involving only inhibitory, gamma-aminobutyric acid (GABA)-dispensing cells can account for many observed spontaneous rhythmic fluctuations measured from the cortex. The brain-wide gamma rhythm observed via intracortical measures is thought to result mainly from GABA receptor activity. However, these models do not include pyramidal cells, which are thought to make up most of the scalp-recorded signals and show robust oscillatory behavior. Thus, spontaneous oscillations in the MEEG signal likely result from an interplay between excitatory and inhibitory cells. Buzsáki (2006) describes neurons as relaxation oscillators, with an "accrual phase" during which the neuron integrates inputs from other cells (this may be equated with the interspike interval). The integration extends until the membrane voltage reaches the threshold and emits an action potential, the duration of which can be seen as the "transmitting phase" (the spike). This process displays phase resetting properties, possibly giving rise to the resets postulated in larger-scale scalp recordings.

In an early report, Treisman (1999) expressed that a plausible mechanism for sensory integration at the neuronal level was synchrony. Other early researchers of brain rhythms shared the notion that different dimensions of an object are bound by tuning in to the same gamma oscillation (Buzsáki, 2006). As we have seen, this hypothesis has received substantial backup from electrophysiology experiments. Moreover, it has been shown that neural synchrony can serve as the integrating mechanism for building complex representations by organizing their subparts, not only in vision (Hummel & Biederman, 1992) but also in more complex reasoning (Doumas et al., 2008; Hummel & Holyoak, 1997; Shastri, Ajjanagadde, et al., 1993). This idea coincides with confirmation of the feedforward-feedback dissociation between high- and low-frequency (gamma and alpha/beta) oscillations, respectively, from nonhuman primates to humans. Michalareas et al. (2016) used MEG to test this relationship, confirming both the frequency dissociation between top-down and bottom-up signals and the hierarchical organization of visual processing in the human cortex.

3.2.2 Oscillations at the scale of the cortical area

Separate cortical areas present different "natural" frequencies but may use them to communicate (Friston, 1997; von Stein et al., 2000). In a seminal paper, Rosanova et al. (2009) perturbed cortical areas the same way one would pluck a guitar string to identify its resonating frequencies. They applied single-pulse transcranial magnetic stimulation (TMS) to the cortex while recording

EEG. They reasoned that the single pulse would make the region "resonate" at its natural frequency. They found that a single pulse of excitation in the posterior lobe evoked alpha oscillations (8-12 Hz). In the parietal lobe, evoked oscillations were in the beta band (13-20 Hz). Finally, when stimulation was applied in the most anterior region, the frontal cortex emitted high-beta and gamma oscillations (21-50 Hz). This study is not the first to find that alpha serves as the natural frequency band of visual regions. Others also found a strong correlation between alpha rhythm and occipital cortical activity thanks to simultaneous EEG and fMRI recordings during rest (Feige et al., 2005; Laufs et al., 2003; Mantini et al., 2007). Rosanova et al. (2009) also performed source localization to measure the frequency evoked in each one of the three areas while stimulating at one cortical location. They found that each lobe resonated at its natural frequency (low for posterior to high for anterior), regardless of where the TMS was applied. These results indicate that spontaneous oscillations accelerate towards the frontal lobe.

In opposition with this result, Kanai et al. (2010) report that when stimulating the visual cortex with tACS, excitability was only raised when stimulating at 20 Hz. Stimulation at other frequencies did not affect the detection threshold. These seemingly contradictory findings suggest that the mapping between oscillatory frequency, cortical area, and cognitive function is highly complex and cannot be reduced to simple, linear relations. It seems to depend on the specific task at hand: even two similar paradigms, involving similar manipulations of cortical excitability, do not yield the same results. We will present our novel tests of these relationships in Chapter II.

3.3 Oscillations correlate with perception and attention

The highest frequencies that have been correlated with cognitive effects are in the beta and gamma bands (> 15 Hz). Gamma-band oscillations have been extensively associated with perceptual binding of features (Fries, 2009; Singer, 1999). Vernet et al. (2019) recently found that high-beta (30 Hz) entraining using TMS significantly improves perception (detection in a visual task). It has also been shown that selective attention enhances gamma synchronization and that this enhancement, in turn, subtends behavioral advantages (Fries et al., 2001). We have introduced the computational model of biased competition, which posits that neurons compete for representation. Attention influences this contest, and evidence suggests that this modulation is implemented via strengthening or suppression of gamma synchrony (Fries, 2009). These are a few among many examples of high-frequency oscillations correlating with perception and attention in humans.

In turn, the lowest frequencies which show correlations with behavioral effects are in the delta band (< 4 Hz). Rhythmic TMS applied at a rate of 1 Hz over the visual cortex for 20 minutes has been found to reduce overall excitability of the visual cortex (Boroojerdi et al., 2000; Wassermann, 1998). Indeed, these low frequencies are typically associated with restful states and low cognitive load (Andrillon et al., 2020; Quercia et al., 2018), including sleep (Terzano et al., 1985).

We now turn to intermediate frequencies in the theta and alpha bands (4 to 15 Hz), which subtend a wide variety of cognitive effects. As made evident in alpha lateralization studies, the alpha band seems to reflect attentional disengagement or suppression. However, the link between alpha oscillations and behavioral performance is substantially more complex.

Even before any event has occurred, both the amplitude and the phase of pre-stimulus, ongoing oscillations can predict detection of a visual stimulus (Busch et al., 2009; Mathewson et al., 2009). This phenomenon is observed when participants do not know when to expect the stimulus, suggesting that spontaneous oscillations reflect fundamental perceptual mechanisms independent of the task or even of volition. The effect is strengthened in the theta band when attention is directed to the location of the stimulus (Busch & VanRullen, 2010; VanRullen et al., 2011). This effect was also found in periodic attentional sampling of visual information in

the alpha band (Dugué & VanRullen, 2014). VanRullen (2016b) presents a substantial body of evidence supporting the theory that perception oscillates at alpha frequencies and that attentional sampling switches from one location to the next at theta rates.

Indeed, frontal theta rhythms were found to correlate with attentional performance and sampling, both using human intracranial electrodes (Helfrich et al., 2018) and nonhuman primate electrophysiology (Fiebelkorn et al., 2018). Fink et al. (2005) also suggest that theta rhythms (6-8 Hz) most closely reflect attentional processes while alpha oscillations (8-12 Hz) correlate more persistently with specific task demands, i.e., the complex cognitive operations one has to perform to complete the task in which they are currently engaged. Babiloni et al. (2004) also show that theta (6-8 Hz) oscillations in frontal and parietal areas display more robust synchronization during an attentional task, whereas alpha (10-12 Hz) synchronization was unaffected by attentional conditions. van Diepen et al. (2016) found that alpha is for easy search whereas theta takes over in difficult attentional search. Busch and VanRullen (2010) also find theta pre-stimulus phase opposition in visual attention.

Overall, theta oscillations are the most promising candidate as an attentional coordination rhythm (Dugué et al., 2019), and alpha oscillations seem closely tied to perceptual processes (VanRullen, 2016b). This observation rests on evidence linking low-frequency oscillations to other neuronal, cortical, and behavioral measures.

In sum, oscillatory frequency plays an important role in the relationship between neural rhythms and cognitive functioning, which can be detected with simultaneous behavioral measures and neural recording. Rhythms ranging from slow (1 Hz) to startlingly fast (100 Hz) have been associated with various perceptual and attentional phenomena. Notably, low-frequency theta and alpha rhythms (4-15 Hz) show robust correlations with these behavioral effects. However, many frequencies seem to be involved in perception and attention. Some do not fit within the simplified delimitations that have been proposed. Thus, the correspondence between neural synchrony and behavior is far from limpid. The first goal of this thesis is to shed light on the temporal dynamics of cerebral synchrony. The second goal is to explore their spatial properties and how the spatial extent of oscillatory activity may influence basic behavioral performance. What evidence has been gathered in the existent literature concerning the spatial dynamics of periodic neural signals?

3.4 Spatial properties of neural oscillations

We have examined the detailed map of attentional control in the primate brain. The spatial structure of attentional neurons and regions seems meticulously organized to boost perception efficiency while remaining highly adaptable. We have also presented evidence of the involvement of oscillations in cognitive functioning. What is the spatial organization of these oscillations in the network? Perhaps oscillations could help communication between and within perceptual and attentional areas? Here, we present the first hypothesis on this topic, which we term the *stationary spatial* hypothesis. In this view, each recorded cortical oscillation is confined to one region, and their interactions are carried out through strictly temporal synchronization. In Chapter III, we will see how theories including oscillatory *traveling* across space provide a new understanding of brain rhythms' spatial dynamics.

Anatomy alone does not suffice to study the brain. The strictly material substrates of the neural system are relatively fixed: mechanical components in the adult brain either stay set or change at prolonged rates, on the order of hours or more. Nevertheless, we are constantly adapting to our environment, switching between tasks, and changing our behavior at consider-

ably higher rates than anatomy alone would allow. Therefore, the brain must involve some fast, dynamic, functional properties that cannot be observed simply from its anatomy. *Stationary spatial* models propose that temporal synchrony contributes to these dynamics by relaying signals from one area to another and structuring the relations between separate regions.

Binding-by-synchrony The different attributes of visual stimuli appear to be processed in different regions along the visual hierarchy (for a simplified example, line orientation seems to be resolved by the primary visual cortex, whereas color is mainly encoded in V4, and more complex movement is processed in the middle temporal area). The general hypothesis of the binding-by-synchrony theory is that the representation of a whole, complex object is mediated by the "concerted action" of these various areas, i.e., that different features of the object are encoded in their temporal structure and bound by the "temporal coincidence of [their] neuronal discharges" (Singer & Gray, 1995). This process is made possible in the view that any two neurons are connected through only a few synapses at most and that most individual neurons receive input from thousands of others. With this in mind, high-resolution temporal synchronization between specific spatial areas can help to increase the saliency of incongruent or unexpected objects by selecting features that belong together and enhancing them for further processing. From the computational side, this selection would be implemented by adjusting spike timing in the system of corticocortical connections. Coordinated timing results in the temporal modulation of discharge rates by alternating between high-summation periods, when all inputs are projected simultaneously (Salinas & Sejnowski, 2001), and low-summation, when all spiking is momentarily silent. In this theoretical framework, multiple cell assemblies even inside a single cortical area can coordinate with each other through different frequencies representing different information. Many experimental reports support this idea of temporal communication within a cortical region (Engel et al., 1991a,b; Gray et al., 1989; Konig et al., 1995), as well as between areas (Roelfsema et al., 1997).

Communication-through-coherence The evidence presented above shows synchronization between neuron assemblies within or between areas, which align with a zero phase-lag, i.e., they alternatively fire and quiet simultaneously. This type of synchronous oscillatory activity has been implicated in perception and attention (Fries et al., 1997, 2008). Bastos et al. (2015) interpret this temporal relation, not as a marker of binding-by-synchrony, but rather to mean that outputting neurons must fire at an appropriate time to arrive at a "good" phase of the receiving neurons and thus produce the highest impact.

In this view, optimal connectivity implies phase-aligned synchronization between the areas of interest. Higher synchronization between V1 and V4 in the presence of attention, compared to unattended stimuli, supports this model (Bosman et al., 2012; Grothe et al., 2012). Lower-frequency (beta) oscillations may support bi-directional connectivity: with longer cycles, the action potentials have enough time to project first in one direction and then the reverse and still land within the same excitatory part of the cycle. Communication-through-coherence is made possible by neuronal assemblies showing intrinsic periodicity (Kopell et al., 2000; Tiesinga et al., 2001), and their local oscillation reflects their excitability (i.e., the probability that they will fire an action potential given their sensitivity to external input; Azouz and Gray, 2000, 2003; Fries, 2005).

The framework of communication-through-coherence was recently updated and extended (Fries, 2015) to include new evidence. In short, this new version can account for selective attention by positing that neuronal assemblies representing an attended stimulus transmit information at just enough higher frequency than unattended ones, so that the transmission from relevant assemblies lands in the short excitatory window in the postsynaptic target. In contrast, the transmission from unattended assemblies lands in the longer inhibition window, thereby silencing their processing. A slow (theta) attentional rhythm would cause a reset of the

gamma alternation in all regions involved, thus regularly ensuring that all transmissions remain in proper phase relations. Finally, the results of gamma-for-feedforward and beta-for-feedback testing are also mentioned, showing that cognitive tasks requiring more top-down control should recruit enhanced beta-band oscillations.

Gating-by-inhibition According to the model of gating-by-inhibition, the brain would inhibit task-irrelevant regions and route the information to task-relevant areas (Jensen & Mazaheri, 2010; Klimesch et al., 2007b; Mathewson et al., 2011). Inhibition would take the form of gating pulses or "blocking" every 100 ms or so (i.e., in the alpha band). It is compatible with the two models of communication between task-relevant regions presented above, simply adding a component of "quieting" of other areas. Phase has long been recognized as the critical property of the alpha rhythm (Varela et al., 1981), and as introduced above in Section 3.3, pre-stimulus alpha phase predicts detection of visual targets. Furthermore, alpha has been found to reflect inhibition countless times (Mazaheri & Jensen, 2010), and is most likely mediated by GABAergic interneuron feedback (Jones et al., 2000; Lőrincz et al., 2009). A recent report from our group (Fakche et al., 2021) demonstrated causal support for the theory of a pulsed inhibition by alpha. These results are the foundation for the model of alpha-mediated gating-by-inhibition. In this context, the higher the alpha amplitude, the larger the inhibition pulses.

Nested oscillations The framework of nested oscillations is also based on the coupling between low- and high-frequency oscillations and constitutes an attempt at unifying gating-by-inhibition and communication-through-coherence while also accounting for feedback circuitry (Bonfond et al., 2017). In this new model, the flow of information is carried by low (theta, alpha, beta) rather than high oscillations, contrary to the previous theories. One important distinction is that alpha has a bipartite role. It delivers pulses of inhibition, as prescribed by the gating framework, but it also supports interareal communication by releasing inhibition, similarly to how gamma was posited to facilitate selective transmissions in the communication-through-coherence model. In the visual network, a decrease in alpha power in the task-relevant regions would create longer windows of gamma-enabled excitability, and two regions engaged in communication would synchronize through coherent phase. In contrast, a region not relevant for the task would show enhanced alpha power (i.e., shorter gamma bursts) and oscillate out of phase. Thus, the irrelevant area's transmissions are suppressed, and relevant communication is rendered highly efficient. If other slow rhythms (theta and beta) are allowed to replace alpha in coordinating interareal communication, the framework can account for results found in many other networks and types of cognitive tasks (see also Phillips & Singer, 1997). The model also ascribes high frequencies to the cortical granular layer and low frequencies to supra- and infra-granular layers to account for feedforward and feedback connectivity.

The models presented here imply synchronization of static signals, each in its localized cortical area. However, these oscillations are prominent enough to reach scalp EEG electrodes, which means the activation of neurons is very strong. Neurons are highly interconnected, and their electric activity spreads outwards: this is the whole basis of electrophysiology. If this were not the case, we would not be able to measure any activity at the level of electrodes. Electric activity propagates outwardly from the source, so there must be at least some signal spreading along the surface of the cortex. Perhaps this spread has a functional purpose? The alternatives to the *stationary spatial* hypothesis posit that cortical activity spreading is functionally relevant to the spatial structuring of signals. We will see these alternatives in detail in Chapter III.

4 The missing keys

We have now covered the theoretical aspects of the existing literature on the relation between perception and attention and its neural underpinnings. We have seen that attention is an essential cognitive function that modulates behavioral and neural measures during perceptual tasks. This influence has been shown using multiple tools such as psychophysics, neural recordings, and non-invasive neuroimaging. We dove into the small-scale neuronal processes of attention and described how attention modulates visual sensory neurons to lay the grounds for describing the attentional network in primates. Methods for wider-scale brain recordings were described and led to a description of attentional implementation in the human brain, which rests chiefly on the characterization of neural oscillations as measured by EEG and MEG. The concept of modeling was introduced to show its merits in better understanding cognitive processes and specifically those involved in attentional control. We presented the leading theories and computational models that account for the existing neurophysiological data. These models guide our understanding of the neural mechanisms of perception and attention and produce valuable predictions for future experimentation. From there, the relation between cortical oscillations and cognition, especially perception and attention, was introduced. A first overarching hypothesis of their spatial organization was presented. This general, theoretical introduction will hopefully guide the reader's understanding of the two experimental chapters.

The aim of this thesis is to provide key insights into the role of brain oscillations in perception and attention. From everything covered thus far, it should become clear that attention needs to be selective, but also highly flexible. Its role is to optimize perception for the task at hand, but it must also adapt to new contexts and highly depend on the current environment. Thus, attention must be able to switch efficiently and quickly between tasks and stimuli. We have indeed shown that attentional processes in the human neural system attest to wide flexibility and adaptability to many tasks. In Chapter II, we will see how the brain may adapt its temporal synchronization to deal with different task demands, and in Chapter III, we will explore how a flexible spatial structuring may help to transmit and process information efficiently.

Overview of Chapter II Most of the studies presented throughout this introduction use a simple, usually binary manipulation of attention ("with" vs. "without" attention, whether it be spatial or object-based). We need to account for more precise attentional effects. By altering the parameters of a visual search, we may describe subtle differences in attentional capture, selection, and sampling. With powerful computational tools at our disposal, we can decompose the phase of neural oscillations to assess precise cortical mechanisms. These tools present the opportunity to explore the neural underpinnings of the behavioral differences between similar but not identical visual search setups. Using a novel paradigm, we were able to test the selectivity of attentional processes in similar but not identical settings (using a blocked design) and its adaptability on a short time scale (using interleaved trials, in which oscillations must re-adapt every few seconds). In Chapter II, we focus on the detailed temporal properties of the neural oscillations involved in visual perception and attention. We present a novel study expanding the already-existing knowledge of the specific frequencies and phase effects on attentional performance. We will see how we explored the link between cognitive mechanisms and neural, temporal oscillations as measured by EEG to explain discrepancies in the literature on this topic.

This study has been posted as a report on the bioRxiv platform and submitted to the international peer-reviewed journal *Scientific Reports* for publication. The report is included within the thesis on page 79. It is identified under the following reference:

Merholz, G., Grabot, L., VanRullen, R., & Dugué, L. (2021). *Periodic Attention Operates Faster During More Complex Visual Search*. Preprint; under review at *Scientific Reports*.

Overview of Chapter III The spatial properties of neural oscillations may also play a fundamental role in cognition. Some evidence exists that spatial phase, frequency, and amplitude affect perceptual and attentional processes, but much is left to speculation. The field needs more evidence of its behavioral impact. In Chapter III, we cover the recent advances in our collective understanding of the spatial properties of cortical waves and show the necessity for a model-based approach to signal imaging. We propose a new method for precise neuroimaging of cortical traveling waves. The experimental work presented in this chapter is part of an ongoing project aiming at a computationally and biologically plausible model of cortical traveling waves. This collaborative project is still in progress but has yielded the poster presentation referenced as:

Grabot, L., Merholz, G., Winawer, J., Heeger, D., & Dugué, L. (2021). Computational Modeling of MEG-EEG Oscillatory Traveling Waves In Human. *Groupe de Recherche (GDR) Vision Annual Conference*.

II

TEMPORAL DYNAMICS

1 Introduction

The body of evidence on cognitive sampling presented in the General Introduction (Section 1.3.3) can be interpreted to mean that low-level perception samples the visual field at rates in the alpha frequency range, and that attentional sampling selects relevant stimuli one after the other at rates falling within the theta range (VanRullen, 2016b). Throughout this chapter, we will see how the relationship between cognition and periodicity may be more complex than this generalization. Many studies have contributed to the cognitive sampling theory, using various tasks and paradigms to probe periodicity in visual processing. We will focus on one type of task which has consistently provided crucial data to perceptual and attentional research: visual search.

1.1 Visual search: a major tool to study cognition

Visual search is a category of psychophysical tasks in which the viewer searches for a target item among distractors in a visual array. Any visual objects may constitute the targets and distractors, from simple geometrical shapes to symbols to complex ecological stimuli. The items may appear simultaneously or sequentially and at identical or disparate locations in the visual field. Visual search has been instrumental in informing cognitive scientists on the mechanisms underlying perception and attention and how the visual system operates. Its flexibility in experimental design has allowed for many tests and discoveries, which we will now review in more detail.

1.1.1 Cognitive theory and seminal behavioral findings

Disjunction and conjunction Early cognitive experimenters ignited the visual search literature with their pioneering experiments. Various authors contributed to show that the distinction between disjunction (pop-out) and conjunction (difficult) search, which yield different reaction time slopes according to the number of distractors (flat slope for disjunction and positive slopes for conjunction), can be accounted for by specific characteristics of the search array. In the example from Treisman and Souther (1985), reaction times are much faster when the target possesses a unique characteristic not shared by the distractors (e.g., searching for a Q among O's, where the target is the only item to possess a straight bar). The slope is less pronounced than when the target shares all characteristics with the distractors (in this example, searching for an O among Q's will be much slower because they all possess the same base circle). When a unique characteristic or other property makes the target so salient that it is found with the same speed regardless of the number of distractors, we can speak of a "pop-out" effect, as the target grabs our attention automatically. A pop-out search thus recruits involuntary, exogenous attention, among other types of attention. In that case, the processing of all items is thought to be carried out in parallel (i.e., the observer processes all items simultaneously; Treisman and Gelade, 1980). Difficult search is of particular interest because experimenters may modulate the characteristics of the search array to generate predictions about the reaction time slope, accuracy, and neural measures, as we will see below. A recent study (Becker et al., 2017) supports a relational account of conjunction searches, which emphasizes items' relations to each other as opposed to a more simplistic feature-specific or object-based view.

New measures Wolfe and Horowitz (2017) have shown that features alone are not enough to define the difficulty of a search: their arrangement also plays a substantial role. The primary measure to compare outcomes of different search setups was reaction time, which early experimenters used to index processing efficiency. Reaction time is helpful to plot and compare slopes

against set size for different target-distractor combinations and rapidly assess which combinations induce an automatic "pop-out" effect (flat curve) versus those that require an effortful search through the elements, which adds processing time with each added item (positive slope). Finally, the steepness of the slope gives a direct measure of the difficulty of that particular search setup: those yielding flat or nearly-flat slopes have been termed "parallel" to denote the automatic processing of all items at once. The term "serial" is used to refer to search setups yielding substantial positive slopes (Wolfe et al., 1989, p.1). However, reaction time may reflect multiple processes apart from attention (decision-making, motor processes, and many others). Researchers gradually moved away from this measure in favor of signal detection methods (sensitivity, criterion) to get more precise behavioral clues concerning its cognitive processes. Brain recordings have also proved instrumental in measuring the neural processes subtending visual search.

What drives visual search? Sperling and Melchner (1978) designed a visual search with two categories of items (small and large) and instructed participants to divide their attention equally between the two types. Participants switched back and forth between the two categories, showing successively better performance on one and then the other size category at each trial. This study was one of the first reports of rhythmically fluctuating attentional allocation. It exemplifies the value of visual search tasks in probing periodic sampling of the visual scene. Such periodicity likely reflects neural processes, which may also fluctuate rhythmically, as we have introduced. However, only little is currently known about the link between visual search periodicity and neural oscillations. Schneider and Shiffrin (1977) showed that search performance also depends on more complex and implicit characteristics, such as the overall probability of one stimulus appearing as a distractor or as a target. However, more behavioral evidence on these unusual properties is essential before exploring their neural underpinnings. The priority, for now, is to fully uncover the neural dynamics of the well-established visual search properties and findings emerging from the behavioral and modeling literature.

1.1.2 Theoretical models of visual search

Models of the underlying mechanisms of visual search have been instrumental in understanding perceptual and attentional functioning during these tasks. To explain experimental results obtained in behavioral measures of visual search tasks, some models posit parallel processing of all items, in which the visual system evaluates every item at the same rate, thus completing the processing of identical items at the same time (Eckstein et al., 2000; Palmer et al., 1993). However, a more common view among theoretical models for this type of task includes a step of sequential processing, in which the items are identified or "bound" (see below) one after the other (Desimone & Duncan, 1995; Olshausen et al., 1993; Schneider & Shiffrin, 1977; Treisman & Gelade, 1980). According to these sequential models, if the target does not generate an immediate, automatic response (pop-out), a psychological mechanism akin to a "spotlight of attention" searches the scene sequentially (e.g., one item at a time, or by groups of elements). This spotlight evaluates a selected element or group at each iteration, and the search terminates once the element matching the target is found. Thus, if distractors are added to the array, the search takes longer.

One question which has puzzled researchers concerning the perceptual processes involved in visual search is the "binding problem." How does the visual system manage to correctly and seemingly effortlessly match all of the features (e.g., size, shape, color, texture) belonging to one object and form the complete representation of that object? This process is certainly not effortless from a neuronal point of view: when stimuli are presented outside of focal attention, their features often get misappropriated and swapped between objects (so-called "illusory conjunctions," Treisman & Schmidt, 1982). Feature binding is the central question in object

recognition, which sorely lacks a solid definition (Reynolds & Desimone, 1999). It is of great interest and importance to visual search experiments because object recognition is usually one of the participants' main tasks during a visual search, i.e., identifying each item to distinguish the target from distractors. Because selective attention prevents illusory conjunctions, it has been proposed as a candidate mechanism for feature binding (Reynolds & Desimone, 1999; Spratling & Johnson, 2004). Specifically, selective *spatial* attention may provide the necessary enhancement to focus processing in the areas responsible for the attended location and enable feature grouping (Treisman, 1998).

Treisman (1964) began the movement away from a view of "early-" vs. "late-stage" attentional processing towards flexible, hierarchical attention processes, more in line with neurophysiological evidence of visual functioning. Treisman and Gelade (1980) soon proposed Feature Integration Theory (FIT) to define a possible mechanism of flexible attentional processes. FIT has explained many of the behavioral results obtained from visual search experiments (Treisman, 1998; Treisman & Souther, 1985). Not only does this cognitive model provide a template for the steps towards feature binding, but FIT also outlines possible mechanisms underlying the sequential processing of items during a difficult visual search. According to this theory, a first stage beginning about 100 ms after stimuli appearance and taking place in visual areas would gather fundamental features present in the scene (such as color, motion, orientation; for lists of basic features see Wolfe and Horowitz, 2017; Wolfe, 2014). Visual areas thus identify all basic features in parallel, such that at this first stage, processing four elements takes the same time as processing twenty-five. Once this stage has terminated, the system holds a representation of which features are in the visual field, including a "feature map" for each one which codes for the locations of different features separately (Palmer et al., 2000). In a disjunction or pop-out search, this is usually sufficient: the individual becomes aware of whether the searched feature is present or not, and the search terminates. However, the second stage is needed to locate a whole object, i.e., in the case of conjunction or difficult search. In this second stage, a transfer of information from the individual feature maps to more frontal attentional areas takes place (see Section 2.2.4 in the General Introduction on the human attentional network). Anterior lobes would contain a "master location map" or "saliency map," according to more recent updates to this model (Deco et al., 2002; Itti & Koch, 2001). Feature binding takes place one location at a time in a sequential fashion until the target is found or until all items have been dismissed as distractors, upon which the search terminates.

Perceptual processing of a stimulus, and more specifically assigning a saliency value to it, cannot occur without relating it to its surrounding context. One stimulus may be of high salience within one context (e.g., if it is very different from surrounding stimuli) but not stand out in another (e.g., when it dwells among identical stimuli). The assignment of salience is very rapid and seems independent of the number of items in a visual search (Itti et al., 1998). Therefore, there must be an active, non-linear mechanism in this fast, early perceptual stage. This mechanism would compare locations in the visual field and produce a saliency map. The second, sequential or "attentional" stage of visual search is thought to be guided by this saliency map and to orient first to locations of high salience (Itti & Koch, 2001). Thus, if salience is more easily assigned (for example, when the target is very different from the distractors), the later attentional stage will likely orient to the target very quickly and begin the sequential stage earlier than in the case of a less discriminable target. To our knowledge, this prediction has not previously been tested. Rodriguez-Sanchez et al. (2007) have added to this idea by including the mechanisms of selective tuning (see General Introduction, Section 2.3.2) within attentional search paradigms to explain the detailed neuronal computations performed during visual search. Their augmented model accounts for results from various visual search setups.

In sum, most of the influential models of visual search include a rapid perceptual stage and an attentional stage of iterative communication between anterior and posterior cortical areas. If the information transfer surges back and forth between regions, we should observe

corresponding neural oscillations in the areas involved (Dugué et al., 2015a). How do these predictions hold against empirical recordings?

1.2 Neural bases of visual search

A large body of evidence suggests that corresponding brain oscillations support the sequential iterations posited by visual search models. Oscillatory dynamics in the cortex have repeatedly been found to set a temporal context for micro- and mesoscale neuronal structures. Neural ensembles may follow these background rhythms to successively fire and quiet together, enabling oscillations to mediate perceptual and attentional sampling (Song et al., 2014). Of course, the relation between attentional cycles and neural ones is complex and likely exceeds a one-to-one mapping. For example, evidence from primate electrophysiology (Fries, 2009), in light of behavioral results in visual search paradigms (Dugué et al., 2015b), suggests that during attentional sampling, more than one item (perhaps 3 or 4) are processed at each cycle of theta oscillations (VanRullen, 2013). This example outlines the importance of shedding light on results obtained in humans with nonhuman electrophysiology and vice-versa.

1.2.1 Intracranial electrophysiology

Experimental findings strongly support an iterative transfer process between fronto-parietal and visual areas. Saalman et al. (2007) found that the posterior parietal cortex and earlier visual area MT become synchronized when monkeys orient their attention to a given stimulus within an array of possible locations. Paneri and Gregoriou (2017) have also shown that oscillations in the prefrontal cortex hold a substantial role in attention. Notably, they explain that beyond the FEF and VPA (see General Introduction, Section 2.2.4 for details), the lateral prefrontal cortex as a whole seems to subtend attentional control, as demonstrated by oscillation studies (Gregoriou et al., 2014; Lennert & Martinez-Trujillo, 2013). These findings constitute a solid basis for expecting oscillations in the prefrontal cortex during a visual search task. The same group has also demonstrated that, without a need for neural stimulation, causality can be calculated using synchronization measures, such as Granger causality and inter-trial phase coherence (Paneri & Gregoriou, 2017).

Early attention researchers and theoreticians viewed visual attention as a spotlight, which would focus on one single portion of the field at any given moment. The spotlight would switch between locations as the observer voluntarily shifts their focus, or another stimulus grabs their attention involuntarily. More recent findings seem to suggest that this spotlight is not so localized and can become split across multiple locations (e.g., Mayo & Maunsell, 2016; Müller et al., 2003). Instinctively, this may reflect separate attentional processes. However, evidence instead favors this attentional split as resulting from dynamic and fast (sub-second) attentional sampling processes (Gaillard & Ben Hamed, 2020). Placing neural mechanisms aside for the moment, performance on visual search tasks oscillates at low frequencies from a purely behavioral point of view. For example, the attentional sampling that takes place during a difficult conjunction search seems to occur in the theta (4-8 Hz) range, whereas that occurring in an easy, disjunction task is in the alpha (8-14 Hz) band (Dugué et al., 2017b).

In nonhuman primates, the locus of attention has been found to move back and forth between visual locations of interest at a rate of about 8 Hz (Gaillard et al., 2020). In an experiment where macaque monkeys searched for a specific target to respond and had to inhibit their response to a distractor (go-nogo task), local field potentials (LFP or iEEG) were recorded to show that in the PFC, beta (14-30 Hz) oscillations' pre-stimulus power correlates with faster reaction times (Zhang et al., 2008). This result constitutes further evidence that beta oscillations reflect top-down control over visual areas. Furthermore, alpha and low beta (8-20 Hz) oscillations correlate with slower reaction times in occipital and temporal areas. Thus, alpha power could

correspond to disengagement of visual anticipatory attention.

In other mammals, the alpha rhythm is also related to improved performance while anticipating the appearance of a specific target and strongly correlate with top-down control (von Stein et al., 2000), making these low-frequency bands a complex marker of the neural processes underlying visual search. Indeed, the sequential component described in the theoretical models of visual search received strong support from Buschman and Miller (2009), who found that macaques explored a visual search array one item at a time in an ordered sequence, at a speed of about 25 items per second (beta band). In a separate study, the same group also demonstrated that beta synchronization was robust during a difficult, endogenous search by nonhuman primates (Buschman & Miller, 2007). In the former, the authors used an ingenious task and analysis method to demonstrate that visual search (while searching for a conjunction of features) operates on items sequentially. These results give us every reason to think that models of visual search that include a sequential step are close to accurately describing the process.

As we have seen while introducing the primate attentional network (Section 2.2.3), Buschman and Miller (2007) also showed a dependence of FEF attentional neurons' firing on the phase of the LFP preceding a saccade. Similarly, Bichot et al. (2005) demonstrated that a stronger synchronization in the beta and gamma bands (25-60 Hz), i.e., higher phase-locking of individual neuronal spiking to LFP fluctuations, is observed when the stimulus in the receptive field possesses a searched feature, versus lower phase-locking when it does not. These results are a first indication that not only the power of synchronization, but also its phase relationships, affect neuronal processing. However, this is of little interest if it is not related to behavior. Following this line of reasoning, we will now attempt to show how neural oscillations relate to cognitive functioning during visual search in humans.

1.2.2 Non-invasive human electrophysiology

1.2.2.1 Oscillatory amplitude correlates with visual search

The amplitude (or power, calculated as amplitude squared) of oscillations measured at the scalp's surface has been shown not only to reflect neuronal and cortical processes but, perhaps most importantly, to be directly related to behavior.

Strong amplitude in the alpha band has been repeatedly associated with inhibition or rest (see General Introduction Sections 2.2.4 and 3.3). The inverse relation between alpha power and performance has been extended in part to visual search paradigms. MEG recordings in an object detection task (Vanni et al., 1997) suggest that during scene exploration, the parieto-occipital sulcus sends information to the parietal cortex about the next items or locations to attend, thus forming a repeating anterior-posterior transfer loop. If the visual system is not currently engaged in a search, the parieto-occipital sulcus is considered at rest: this coincides with the emergence of alpha oscillations. Alpha power may thus be a marker for the absence of anterior-posterior information transfer and parietal disengagement. In light of this result and those from other tasks, such as simple visual detection or discrimination, which anti-correlate alpha power to efficient functioning, the overall notion has been that the alpha rhythm reflects inhibition. However, this theory does not explain opposing reports, in which higher alpha amplitude predicted attentional strength and visual activation (Mo et al., 2011).

High oscillatory amplitude correlates with improved performance during visual searching. Tallon-Baudry et al. (1997) found that a 35-38 Hz amplitude increase in the EEG signal, separately in posterior and anterior regions, is apparent in both stimulus-driven perceptual processing and top-down attentional search, suggesting that gamma reflects both feedforward and feedback signals during a visual search. The former seem localized in occipital regions with a slightly lower frequency, and the latter in frontal regions with a higher frequency. A body of research on gamma oscillations corroborates this interpretation and supports the idea that high-frequency rhythms in visual cortices are a marker of elementary visual encoding (Klimesch,

1999). Using a more traditional visual search task, Phillips and Takeda (2009) found that these perceptual and attentional tasks involve high-beta/low-gamma (22-34 Hz) EEG rhythms, partly reproducing the intracranial findings by Buschman and Miller (2007). The authors suggest that these intermediate-frequency oscillations reflect top-down (conjunction) attentional processes and that bottom-up (disjunction) signals yield higher-frequency gamma rhythms. Similarly, von Stein and Sarnthein (2000) showed that different cognitive processes could involve brain oscillations with distinct frequency properties. These notable findings may indicate that neural oscillations support the rhythms observed in behavioral measures.

Regarding lower-frequency cycles, theta oscillations are thought to originate mainly in the hippocampus and to reflect high-level information processing and "will," or "intentional action," including that involved in visual search (for a light review see Buzsáki, 2006, pp.19-21). Besides, as we have seen, we can expect more frontal involvement as the task gets increasingly complex; and more frontal activity is associated with higher-frequency EEG signals (Rosanova et al., 2009). Concurrent EEG-fMRI during resting state showed the same relationships (Feige et al., 2005; Laufs et al., 2003; Mantini et al., 2007). Based on these findings, we may expect higher frequency when the frontal cortex is involved, i.e., when the task is more complex and requires stronger involvement of the FEF, a crucial area for attention (see General Introduction, Section 2.2.4).

In conclusion, the amplitude of neural oscillations reflects fundamental neuronal mechanisms, making it an essential part of cognitive functioning during visual search. One aspect that we have not covered yet, however, is the phase of these cerebral rhythms. The phase of neural oscillations may be the property of oscillatory dynamics that effectively drives cognition.

1.2.2.2 Beyond the classic view: Oscillatory phase as a marker of cognitive functioning during visual search

Power, a measure of an oscillatory signal's peak-to-peak amplitude or "strength," has classically been used to assess oscillations and relate them to neural mechanisms and behavior. Power and amplitude analyses have been instrumental in indicating how neurons depend on certain rhythms, which cortical areas respond spontaneously at which frequency, and which behaviors are associated. However, the information provided by amplitude alone is quite limited. It can inform us generally of the frequencies involved in each process, but it cannot provide a precise temporal measure of how these processes relate to the oscillation's timing, i.e., its phase. Phase can be thought of as the instantaneous amplitude of the oscillation or the absolute intensity at the specific time point of interest (see Figure II.1.1).

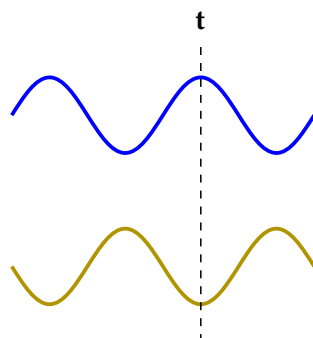


Figure II.1.1: Two oscillations have the same amplitude, but not the same instantaneous phase. At time t , the blue oscillation (top) is at peak phase, whereas the yellow oscillation (bottom) is at trough phase.

In more recent years, phase analyses have become a key measure to shed light on exactly

how neurons and cortical areas may use the oscillations uncovered by power analyses to operate and communicate with each other for maximally efficient cognition. Specifically, phase analyses allow us to know which parts of the oscillatory cycle are critical and precisely relate one oscillation to behavior in a definite temporal relationship—the following section reviews critical findings in phase measures of brain oscillations. We will attempt to clarify how phase affects or reflects neuronal activity and how this translates to cortical area synchrony, finally impacting cognition during visual search.

The phase of high-frequency oscillations reflects neural processes In the same study presented above, Tallon-Baudry et al. (1997) found that gamma-band (38-54 Hz) oscillations phase-lock to the stimulus during a perceptual task (searching for a target shape within a texture). Similarly, Phillips and Takeda (2010) found that while performing the same classic visual search paradigm as in their 2009 study (see above), elderly individuals are more subject to exogenous attention, i.e., "more easily captured," and they exhibit more high-gamma phase-locking. This result indicates that the phase alignment of gamma oscillations is a marker of bottom-up, exogenous attentional control.

Beta oscillatory phase has also been found to impact visual performance in humans (Fiebelkorn et al., 2013). Phase synchrony between the FEF and LIP (mainly in higher frequencies, 20-55 Hz) is associated with attentional control during a visual search task (Buschman & Miller, 2007). The more challenging the task (recruiting "top-down" control while searching for a conjunction of features), the greater the synchrony between frontal and parietal cortex in the high beta band (22-36 Hz). If the task is effortless ("bottom-up" pop-out), phase synchrony in the gamma band increases.

Therefore, searches in which an attentional effort is needed seem to require low-frequency phase communication. Beta synchrony effects are replicated in humans using EEG and phase-locking value analyses (Phillips & Takeda, 2009, for details on these methods, see Section 1.3 below). A human study involving transcranial magnetic stimulation (TMS; Chanes et al., 2013) also reports these effects in both bands, showing that stimulating the FEF in high beta (30 Hz) and gamma (50 Hz) frequencies with a regular, rhythmic pattern improves detection performance compared to stimulating with a random, arrhythmic pattern. Together, these results demonstrate the causal role of high-frequency oscillations in perception and suggest a requisite function of the temporal phase.

Similarly, the data from a visual search study in humans suggest that strong phase-locking between anterior and posterior regions in high-beta and low-gamma bands subserves visual integration (Phillips et al., 2012). The participants performed visual search tasks for targets composed of either one, two, or three conjunctions between target and distractors. The authors measured the phase-locking between frontal and parietal cortices to find that it becomes significant in the high-beta/low-gamma band, including when comparing only conditions with similar accuracy and reaction time (i.e., the difference is not due to task difficulty). Together, these results constitute strong evidence that high-frequency oscillatory phase affects individual neurons and neuronal ensembles, thus impacting cognitive functioning during visual search tasks down the line.

The phase of low-frequency neural rhythms reflects perception and attention Early studies separated participants' reaction times to simple stimuli by alpha phase bin and found that the instantaneous phase of this easily-recorded cycle significantly correlates with behavior (Callaway & Yeager, 1960; Dustman & Beck, 1965; Lansing, 1957). Soon, research showed that detection itself also depends on alpha phase (Nunn & Osselton, 1974; Varela et al., 1981). O'Keefe and Recce (1993) made the startling discovery that hippocampus place cells in rats show phase precession or recession while the animal is in motion. These place cells fire in a different phase of the LFP theta/alpha rhythm (4-12 Hz) according to whether the animal is

entering or exiting the location coded by the cell. The phase also reflects the animal's distance from this location. This finding constitutes crucial evidence of the importance of phase in low-frequency neural rhythms. Evidence has accumulated in favor of the conclusion is that beyond spike-count averages, spike *timing* relative to the phase of ongoing, background network fluctuations also significantly codes for information (Wang, 2010). The oscillatory phase of electromagnetic brain signals may, for example, reflect local circuit functions and connect them via inter-areal communication over long distances (Buzsáki, 2006; Fries et al., 2007; Schneider et al., 2006).

At the level of larger neuronal ensembles and cortical areas, Fiebelkorn and Kastner (2019) have described the phase relation between theta oscillations (3-8 Hz) and spatial attention, showing that accumulated evidence from visual search and other paradigms supports theta-anchoring of other neural rhythms and of behavior. One particular phase of the theta oscillation seems to reflect increased excitability, thus improving perceptual processing, whereas the opposite phase would indicate a period of attentional switching to another item or location. This latter shifting phase would accompany an increase in alpha power, which likely reflects a temporary inhibition of perceptual processing. In this view, the theta rhythm is driven by the frontal eye fields (FEF), one of the areas of highest complexity along the attentional pipeline (see Section 2.2.3). Alpha inhibition is, in turn, most evident in the lateral intraparietal sulcus (LIP). This framework implies a strong top-down involvement of fronto-parietal areas' oscillatory phase during visual search.

Finally, low-frequency phase also seems to reflect macro-level, cognitive and behavioral effects of low-frequency phase. The phase of ongoing and stimulus-induced low-frequency oscillations is thought to reflect working memory processes, which are likely involved in visual search (Jensen & Lisman, 1998; Lisman & Jensen, 2013). Barry (2003) report that during an auditory oddball experiment akin to a sequentially presented visual search task, the phase of low-frequency (1-13 Hz) neural oscillations was non-uniformly distributed around stimuli onset. The authors interpret this to mean that the neural system dynamically adjusted its fluctuation so that stimuli onset would occur in a preferred phase (most likely reflecting an optimal brain state). In the case of a complex target-searching task in the auditory modality (Kolev et al., 2001), phase-locking across trials in the alpha band is strongest after 500 ms following stimulus onset and localized in frontal electrodes. This evidence from an auditory task supports the involvement of alpha phase in complex brain processes. We will now see how the pre- and post-stimulus phase of neural oscillations relates to cognition during visual search.

Pre-stimulus phase determines search performance Hanslmayr et al. (2013) recorded EEG and fMRI simultaneously while participants searched for a target contour within an array of oriented patches (Gabor stimuli). They found that the phase of 7 Hz spontaneous oscillations (preceding stimuli onset) significantly predicts accuracy in indicating whether a contour was present or absent. This task is similar in structure to classic visual search paradigms but was specifically designed to activate low-level visual areas coding for Gabor orientations (occipital lobe) and high-level parietal areas such as the LIP, which serve to integrate orientations over large spatial expanses. Thus, the rhythmic 7 Hz fluctuation is interpreted to reflect iterative communication windows between occipital and parietal poles to enable a sequential attentional sampling of the visual scene. Although this study did not explicitly test the predictions of visual search models, it provides additional evidence in favor of rhythmic, sequential sampling during attentional search.

Direct evidence for a rhythmic sampling of the array during visual search comes from our group (Dugué et al., 2015a). Participants were asked to report whether their target was present or absent in a visual search task (looking for a T among L's). They found opposite pre-stimulus phases in the theta band (~6 Hz) for correct and incorrect trials. This result provides direct support for the rhythmic attentional sampling theory, and the most parsimonious

technical explanation for this periodicity is the sequential processing of items in succession. This interpretation is reinforced by the fact that pre-stimulus phase opposition is most prominent in occipital and parietal sites in this visual search paradigm. These two regions may engage in communication during attentional sampling, as described by the models presented above. Finally, pre-stimulus phase opposition was weaker when the task was less complex, although it peaked in the same frequency band as the original difficult search. A natural question flowing from this last result is whether the pre-stimulus phase would even more strongly affect search performance given a more complex task. Besides this, other differences in time-frequency decomposition profiles may exist between search setups with different characteristics (search difficulty, set size), but they have not yet been tested.

Post-stimulus phase determines attentional efficiency Stimulus-induced ERPs may reflect resetting of ongoing oscillations (Barry et al., 2000; Brandt, 1997; Jansen & Brandt, 1991). Specifically, this reset seems to reflect top-down processes more robustly than bottom-up ones (David et al., 2005; Klimesch et al., 2007b; Shah et al., 2004). Phase synchrony in the alpha band between distant cortical areas was also found to be present during top-down processing (Klimesch et al., 2007a; Sauseng et al., 2005b; von Stein et al., 2000).

In the previous section, we have seen the effects of pre-stimulus phase, i.e., the instantaneous amplitude of ongoing oscillations before the search array appears, on attentional performance. It seems unlikely from these consistent effects that the spontaneous oscillations take no part in the ERP. What are the effects of phase once the array has appeared, i.e., in the post-stimulus period? In a first study, our group (Dugué & VanRullen, 2014) showed that search efficiency on a difficult conjunction task, in which participants needed to perform a mental operation on the stimuli to find the single appropriate combination of color and orientation, fluctuated periodically over time at a rate of about 10 Hz (alpha). This periodic sampling started at a similar phase (relative to stimulus onset) for all participants. Again, such periodicity in attentional performance was not evident in an easy, pop-out task (searching for a + among L's), suggesting that sequential, iterative feature integration (as posited by classic models of visual search) is only required in search tasks which surpass a certain level of complexity or difficulty. Together, these results would lead one to expect stronger post-stimulus phase-locking in difficult than pop-out visual search, when frontal and parietal regions are recruited to direct processing in the occipital pole, thus engaging a strong top-down feedback loop. To date, the only test for this prediction comes from Dugué et al. (2015a). Indeed, the phase-locking difference in the theta band between correct and incorrect trials was weaker on the easy task than the difficult one. Interestingly, this measure for oscillatory resetting was most concentrated in occipital and frontal regions during the difficult search, suggesting that iterative communication was occurring between posterior and anterior regions as posited by visual search models.

Towards a better characterization of oscillations in visual search Much more specific characterization of the relationship between visual search and neural oscillatory phase is needed. Many questions regarding this relation remain unanswered. As we have seen, frequency reports from various studies seem to contradict each other. These are difficult to compare because they use different tasks and are not carried out in the same, controlled environment. It is possible that even subtle differences in item arrangement affect which frequencies are recruited and when. Oscillatory characteristics such as phase-locking and pre-stimulus phase opposition may support different types of visual search. How specific are these effects? We set out to address these questions by recording EEG while participants perform visual search tasks. Our aim is to assess the link between oscillatory phase and search performance. Many methods have been described to analyze pre- and post-stimulus EEG oscillations, but some have proven more efficient and reproducible than others. What are the most conclusive ways to estimate phase?

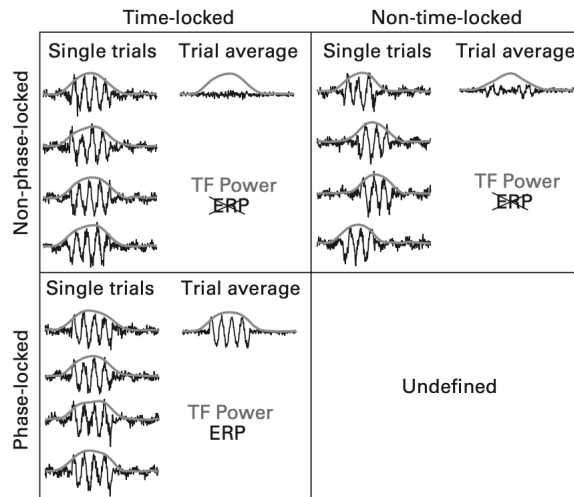


Figure II.1.2: The calculation determines which components of the signal are captured. In each cell, four trials of simulated data are averaged. Black traces represent unfiltered time courses and gray traces represent the amplitude of 10-Hz power. Evoked response potentials (ERPs) can only capture phase-locked activity, whereas time-frequency (TF) power also captures non-phase-locked signals. Reproduced from Cohen (2014).

1.3 Optimal methods to extract time-frequency power and phase

1.3.1 Time-frequency decomposition by Morlet wavelet

The evoked response potential (ERP) captures only activity that is both phase-locked and time-locked (Figure II.1.2). However, another calculation can yield more explicit information across trials: time-frequency decomposition. This method makes use of convolution (see Figure II.1.3) to extract precise amplitude and phase information from raw signals. The underlying assumption is that seemingly complex signals such as those measured by the electroencephalogram are a sum of many simple signals, i.e., pure sinusoidal components with many frequencies, amplitudes, and phases (Figure II.1.4). Convolution of the raw EEG signal with a sine wave allows us to calculate how strongly that particular wave (with its frequency, amplitude, and phase) is represented in the signal. However, convolution with a whole sine wave results in edge artifacts and imprecise amplitude and phase estimations. For these reasons, it is optimal to take only a few cycles of the sine wave of interest to create the smaller "kernel" of the convolution, and to taper off its edges to zero, an operation usually achieved by applying a Gaussian (or equivalent) window to the shortened wave. The result is the Morlet wavelet, which, when convolved with the raw EEG signal, yields an illustration of the representation of the sinusoid of interest in the signal. Typically, this calculation is taken one step further by adding the imaginary dimension, thus yielding a complex vector for each frequency of interest at each time point of the signal.

1.3.1.1 Extracting amplitude and single-trial power

The length of the complex vector yielded at each time-frequency point by the Morlet wavelet convolution corresponds to the oscillatory amplitude for the sinusoid in that frequency. Power is calculated as amplitude squared, so when using power, one must correct for the $1/f$ power relation (Buzsáki, 2006). However, it is possible to avoid this problem by taking the amplitude

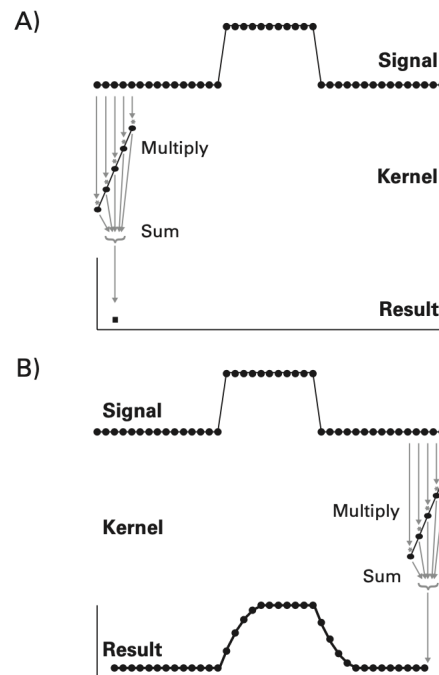


Figure II.1.3: Illustration of convolution. At each step, the dot product of the kernel and corresponding segment of the signal is computed. The kernel "slides" point by point along the data, from the start of the time course (A) to the end (B), yielding the dot product at each segment until all points have been accounted for. This sliding window calculation means that multiple signal points contribute to each point in the convolution result (bottom). Therefore, there is some overlap between neighboring points, resulting in partially smoothed curves. Reproduced from Cohen (2014).

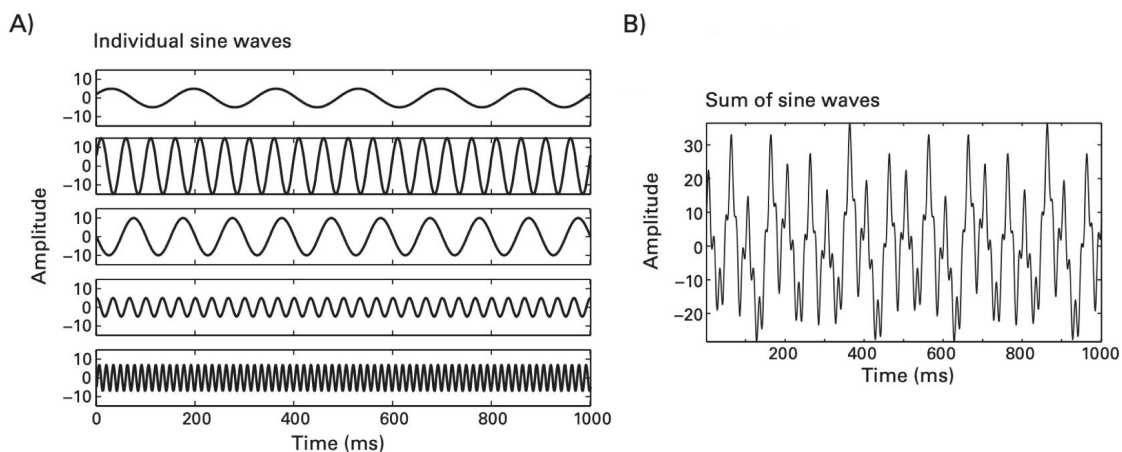


Figure II.1.4: When summing individual sine waves with different frequencies, amplitudes, and phases (A), the resulting signal quickly gains in complexity (B). Reproduced from Cohen (2014).

directly, in which case permutation or bootstrapping correction procedures combined with corrections for multiple comparisons such as the False Discovery Rate (FDR) method (Benjamini & Hochberg, 1995) are best adapted, especially with somewhat low numbers of trials or participants (Cohen, 2014). The bootstrapping procedure artificially shuffles trials to create

a null distribution and thus allows assigning a z-score to the ordered data, which are then converted to p-values. FDR then corrects for multiple comparisons by sorting the p-values (one for each time point) and assigning a threshold based on the total number of points, a threshold typically reduced by setting an $\alpha < 1$. If any survive, the highest p-value becomes the FDR-thresholded cutoff; if not, the threshold is set to 0, and no p-values survive the test. As opposed to the ERP, in which the calculation involves averaging the signal of all trials together and measuring the amplitude or power of this averaged signal, this calculation yields highly accurate and informative "single-trial" amplitude, meaning the amplitude is measured at each trial individually and only then averaged (VanRullen, 2016a). The signal itself sustains no alterations.

1.3.1.2 Phase analyses: how should phase be extracted?

One traditional method to evaluate phase in EEG signals has been to filter the raw data at or around the frequency of interest, making it easy to visualize and calculate phase. However, this method removes much information from the original data and still relies on signal averages, making it less precise than Morlet wavelet convolution (Lachaux et al., 1999). A more precise alternative is inter-trial phase coherence (ITC), sometimes referred to as clustering (Cohen, 2014). In short, ITC measures how clustered the complex vectors are around any angle (phase) at every time-frequency point across trials, regardless of their length (amplitude), which is normalized (see phase circles in Figure II.1.5 for an illustration). ITC, filtering, and the ERP all capture phase-locked activity, but ITC allows for more frequency and phase precision. This is because ITC takes the instantaneous phase at each trial (as opposed to the averaged signal in the ERP). Thus, ITC can detect very short bouts of phase-locking, whereas the ERP cannot.

Most importantly, if we filtered and plotted the ERP, we would not be able to distinguish whether a low-amplitude oscillation resulted from a strongly-phase-locked, low-amplitude signal or a weakly-phase-locked, high-amplitude signal. ITC tells us precisely which signals are strongly- vs. weakly-phase-locked. The amplitude of the ERP comes from both the amplitude and the phase of single-trial responses. From the average alone, we can never know to what extent each one contributes. Thus, separating the phase and amplitude analyses can better inform us on what we are measuring and yield precise information about the EEG signal.

1.3.2 Pre-stimulus Phase Opposition

One of the first papers to report a pre-stimulus phase effect of ongoing oscillations on detection performance (Busch et al., 2009, see above) used the Phase Bifurcation Index (PBI) to calculate phase opposition. The PBI takes the ITC of both outcomes (here, detection and miss) into account and allows for a quantification of phase effects over large frequency bands and time periods. However, these and other authors have since moved away from this measure in favor of Phase Opposition Sum (POS; see Figure II.1.5, left), which is calculated as

$$ITC_A + ITC_B - 2 * ITC_{all}$$

where A represents one outcome (e.g., detection) and B represents the other (e.g., miss). By subtracting the phase coherence of all trials combined, POS has the advantage of controlling for non-uniformly distributed (i.e., non-spontaneous) phase patterns. Indeed, if the two outcomes both show strong phase-locking (high ITC) but are not in phase opposition, the overall phase clustering (both outcomes combined) will be skewed to one side, and ITC_{all} will also be high. Thus, a high POS value indicates that the two outcomes exhibited fully opposed phase-locking. Note that POS only takes into account the relative phase between outcomes and never the actual phase values. This is because the EEG phase is only indirectly related to the underlying neural oscillations, so interpreting its absolute phase would yield unfounded conclusions (VanRullen,

2016a).

In experiments involving pre-stimulus phase estimation, introducing an inter-trial temporal jitter is crucial because if the participant were to know when to expect the subsequent trial, they might align oscillations to this expectation across trials, and their phase would no longer reflect truly spontaneous rhythms (Busch et al., 2009; Busch & VanRullen, 2010; Dugué et al., 2011, 2015a). This idea often brings up the question: How can there be an effect before the stimulus even starts? If the participant does not know what they will see or when in advance, should effects not cancel out? Participants do not need to know anything in advance, because we artificially cut the trials post-hoc relative to stimulus onset and label them as one outcome

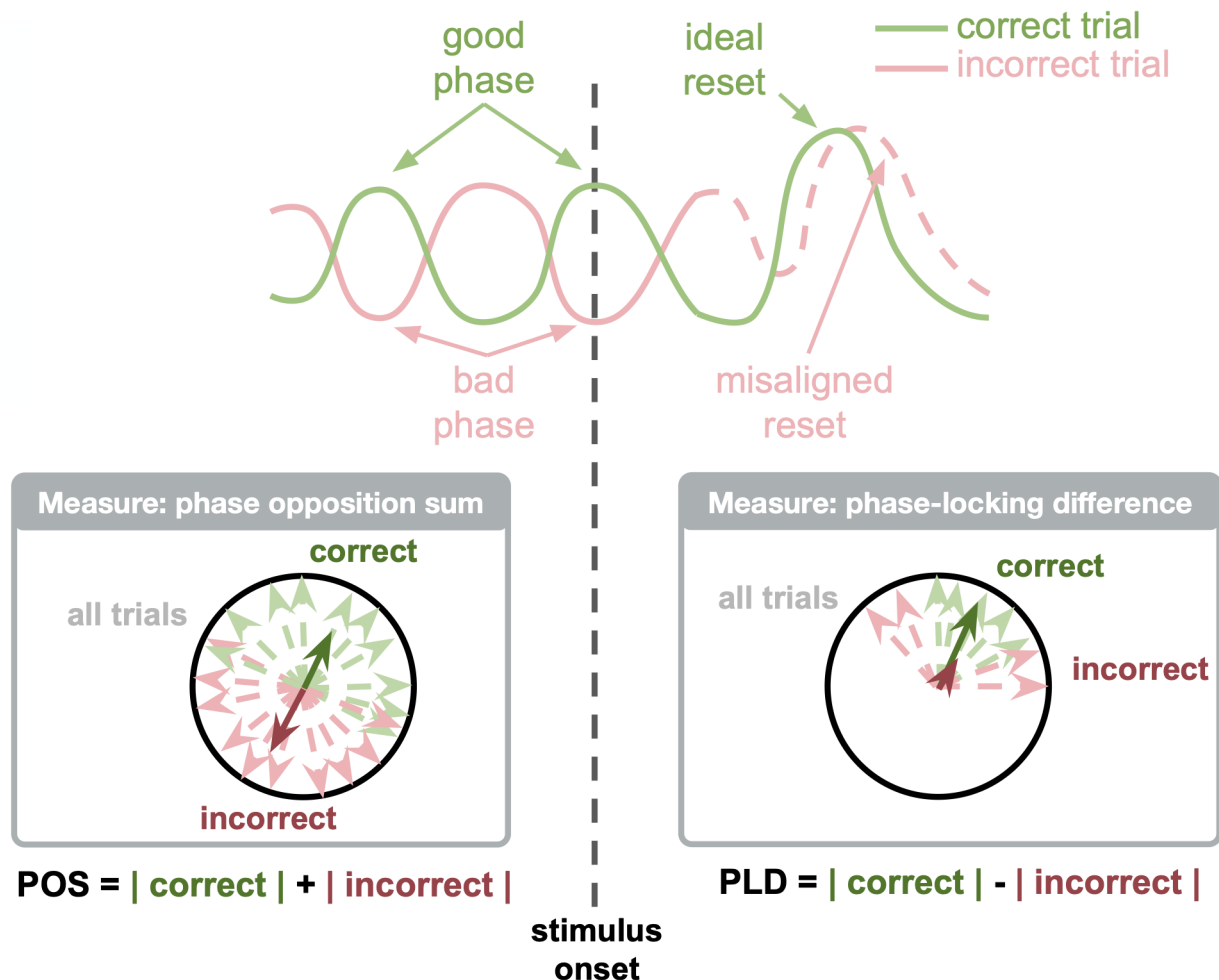


Figure II.1.5: Illustration of POS and PLD. The calculations for phase-opposition sum (POS) before stimulus onset (left) and phase-locking difference (PLD) after stimulus onset (right) are depicted. Top traces correspond to example theoretical oscillations from a correct trial (green) and an incorrect trial (pink). Phase-amplitude vectors extracted by Wavelet convolution are depicted in the bottom boxes. Pale dashed arrows represent individual trials' vectors: the length is normalized to 1 to remove any influence of amplitude and the angle corresponds to instantaneous phase. Dark arrows represent the averaged vectors and correspond to inter-trial phase coherence (ITC). POS is calculated as the sum of the length of average vectors for correct and incorrect outcomes (the subtraction of the overall ITC is not shown for simplification). PLD is calculated as the subtraction of the incorrect average vector's length from the correct one.

(e.g., detection, miss, correct, incorrect). Therefore, based on the trial's outcome (its label), we can correlate any effect from the pre-stimulus period that might have been beneficial or harmful to the participant's performance.

1.3.3 Post-stimulus Phase-Locking Difference

Phase resetting of ongoing neural signals participates in visual attention. Indeed, it has been found more likely in high-level attentional processes, but less so in occipital low-level visual ones (Shah et al., 2004). This finding suggests that phase resetting subserves complex cognitive functioning, such as that recruited during difficult visual searches requiring effortful attentional processes. Thus, post-stimulus phase-locking may be a critical measure for linking these processes to their underlying neural substrates. While using visual search tasks, the question of interest is whether phase resetting has any impact on task performance, i.e., if participants are more likely to correctly determine the presence or absence of their target when the reset is closer to optimal (see Figure II.1.5, right). Because ITC gives the most precise estimation of instantaneous phase clustering across trials, it may also be used to reveal the precision of the reset. Finally, to determine the extent to which correct trials sustained an advantage from the reset, we subtract the ITC for incorrect trials from that for correct trials to obtain Phase-Locking Difference (PLD):

$$ITC_{correct} - ITC_{incorrect}$$

This calculation allows us to test the hypothesis that a stable reset across trials characterizes correct trials. In contrast, incorrect trials would depart from the optimal search resetting and thus exhibit more dispersed instantaneous phases across trials, i.e., weaker phase-locking (Dugué et al., 2015a). Because this subtraction is performed at every time-frequency point, it is also crucial to bootstrap and correct for multiple comparisons, as in the POS calculation (see previous section).

1.4 The present study

We have seen that attention and perception seem to sample the visual environment periodically at low frequencies. Furthermore, periodicity in attentional and perceptual processes are likely a reflection of brain oscillations in similar low frequencies. An inspection of attentional and perceptual sampling studies reveals that within low-frequency bands, large discrepancies exist between the frequencies reported across the literature. These disparate results may be explained by the variety of tasks administered, each one demanding a different degree of attentional involvement. Our hypothesis is that the heterogeneity of frequencies reported in previous studies results from this variability in task demands. Our aim with the present study was to test the link between attentional demands, periodic sampling and neural oscillations. We elected to test this relationship using visual search tasks, which allowed us to manipulate task parameters in a controlled manner to investigate the impact of varying task demands. In a first experiment, we modulated target discriminability, with three target-distractor shape combinations. In the second experiment, we adjusted the number of distractors, with two set size conditions in a separate experiment. We recorded electroencephalography (EEG) while participants performed the visual search tasks in order to link phase-locking effects to the cognitive conditions, and match neural activity with the systematically manipulated attentional demands in our two experiments. Our first prediction rests on oscillatory frequency: more complex searches should demand more samples of the visual field and require more frontal involvement in order to successfully process all items. Thus, we predicted that more complex search setups (lower target-distractor discriminability and more numerous distractors) would show higher-frequency pre-stimulus phase opposition and post-stimulus phase-locking difference. Additionally, if attentional search is guided by salience as posited by classic models of visual search, then

post-stimulus phase effects should arise later when salience is harder to assign, i.e., in the more complex conditions. We computed pre-stimulus phase opposition and post-stimulus phase-locking difference as described above in an effort to elucidate the role of oscillatory phase in the link between attentional sampling and neural activity.

2 Article

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1 **Periodic attention operates faster during more complex visual search**

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8 9 10 11 **Abstract**

12 Attention has been found to sample visual information periodically, in a wide range of frequencies
13 below 20 Hz. This periodicity may be supported by brain oscillations at corresponding frequencies.
14 We propose that part of the discrepancy in periodic frequencies observed in the literature is due to
15 differences in attentional demands, resulting from heterogeneity in tasks performed. To test this
16 hypothesis, we used visual search and manipulated task complexity, i.e., target discriminability
17 (high, medium, low) and number of distractors (set size), while electro-encephalography was
18 simultaneously recorded. We replicated previous results showing that the phase of pre-stimulus
19 low-frequency oscillations predicts search performance. Crucially, such effects were observed at
20 increasing frequencies within the theta-alpha range (6-18 Hz) for decreasing target discriminability.
21 In medium and low discriminability conditions, correct responses were further associated with
22 higher post-stimulus phase-locking than incorrect ones, in increasing frequency and latency.
23 Finally, the larger the set size, the later the post-stimulus effect peaked. Together, these results
24 suggest that increased complexity (lower discriminability or larger set size) requires more
25 attentional cycles to perform the task, partially explaining discrepancies between reports of
26 attentional sampling. Low-frequency oscillations structure the temporal dynamics of neural activity
27 and aid top-down, attentional control for efficient visual processing.

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28 Introduction

29 Covert attention selects task-relevant stimuli among the constant flow of sensory information
30 (in the absence of eye and head movement) to facilitate their processing [1-3]. A large literature
31 (for review [4-8]) shows that spatial attention samples visual information periodically at low
32 frequencies, i.e., < 20 Hz [9-19] and that this sampling is supported by brain oscillations at
33 corresponding frequencies [20-23]. Critically, the frequencies reported in the literature show fairly
34 large discrepancies, which to date remains understudied. One parameter that may be involved is
35 attentional demand, as it was shown to correlate with neural activity in posterior and frontal areas
36 [24], visual neuronal activity [25], and with individual alpha peak frequency [26]. Here, we explicitly
37 tested whether the variability in frequencies reported across the attentional sampling literature may
38 be due to varying attentional demands, potentially caused by the disparity of tasks.

39 Visual search tasks — looking for a target among distractors — have been largely used to
40 study attention (for review [27,28]), and more specifically its temporal dynamics. A periodic
41 attentional mechanism implies cycles of discrete sampling windows over time. Visual search is
42 particularly adapted to test the link between these attentional cycles, neural oscillations and task
43 demands, because task demands may be easily manipulated by varying target discriminability
44 among distractors or varying the number of distractors.

45 It has been proposed that attentional sampling during visual search tasks rests on periodic
46 neural activity [5,7,20,29,30]. Particularly, it was shown that the pre- and post-stimulus phase of
47 theta oscillations (4-8 Hz) distinguished correct from incorrect trials [20]. Interestingly, when
48 disrupting low-level occipital (V1) and high-level attentional (FEF) areas in humans using
49 transcranial magnetic stimulation (TMS), performance was modulated periodically at low
50 frequencies (< 20 Hz) [20,29,30]. This result was interpreted as evidence that the sampling process
51 of attentional selection during visual search is periodic and is supported by brain oscillations at low
52 frequencies.

53 Here, we recorded electro-encephalography (EEG) during visual search tasks with varying
54 attentional load to test the link between brain oscillations and task demands, and further
55 characterize periodic attentional sampling. We first replicated previous results showing that pre-
56 stimulus phase [20,31-40] and post-stimulus phase-locking across trials [20,41] of low-frequency
57 oscillations predict successful task performance (same task as in [20]). Specifically, the phase of
58 spontaneous oscillations (before stimuli onset) predicts trial outcome; and post-stimulus phase
59 alignment (phase-locking) aids performance, which we call phase reset here to refer, strictly, to the
60 mathematical description of the effect [42].

61 Crucially, we tested the prediction that an increase in the number of cycles required to perform
62 the search would result in an increase in the frequency of the underlying neural oscillations, and/or
63 in a delayed peak of the neural response. Specifically, we manipulated the discriminability of the
64 target (Experiment 1) and the number of items in the search array, i.e., set size (Experiment 2). Our
65 working hypothesis was that during one attentional cycle only a limited amount of information from

66 the search array is processed – either because not all stimuli are attended at once, or because
67 attention is divided among all stimuli and thus less resources are attributed to each stimulus (here,
68 we do not aim to disentangle these two options). It follows that given a fixed search duration, the
69 more complex the search task, the higher the frequency of the neural oscillation required for
70 successful performance – allowing more cycles to be completed in the same amount of time.
71 Moreover, alpha/theta phase realignment has been associated with more efficient sensory
72 processing of targets [20,43]. Therefore, if lower discriminability and additional items entail more
73 attentional cycles, and if phase-locking aids performance while processing the target, a delayed
74 phase reset can be expected, to allow for a periodic sampling process to cycle through the search
75 array and complete the processing of the target.

76 In Experiment 1, the target and distractors' shapes were manipulated to obtain three levels
77 of discriminability (high, medium and low, with equalized task performance; blocked). We tested
78 two predictions: (1) the lower the discriminability, the higher the frequency of the pre- and post-
79 stimulus brain oscillations underlying attentional performance; (2) the lower the discriminability and
80 the later the optimal phase reset, resulting in delayed post-stimulus temporal dynamics. Indeed,
81 some phase resetting is to be expected simply due to stimulus onset [42,44], but a stronger reset
82 should lead to better performance [20], hence higher phase-locking is expected in correct trials.
83 Furthermore, if the search requires on average more attentional cycles, as hypothesized when
84 increasing search complexity, then this would translate in an optimal phase reset that appears at a
85 delayed latency.

86 In Experiment 2, the set size (number of items in the search array, 4 or 8; interleaved) was
87 manipulated. Here, we tested a last prediction: (3) the optimal phase reset affecting behavior occurs
88 at a delayed latency and higher frequency when more items are presented (i.e., higher task
89 complexity). Because the participant cannot predict the set size of the upcoming trial, we did not
90 expect an effect of set size on pre-stimulus activity and thus did not test it – there is no reason to
91 assume here that participants can adapt their sampling frequency in advance.

92 Altogether, the results confirm our three predictions and suggest that increased attentional
93 demands requires more attentional cycles to perform the task (higher frequency), partially
94 explaining discrepancies between reports of attentional sampling.

95

96 **Results**

97 **Behavior**

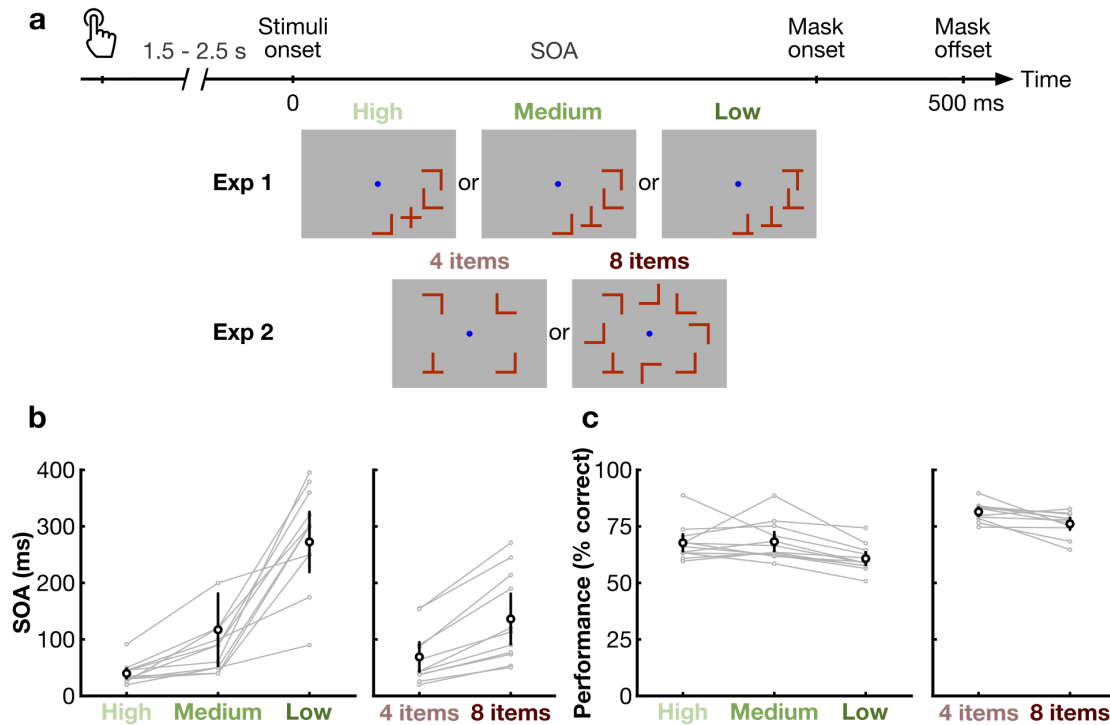
98 Participants performed a visual search task with varying parameters while
99 electroencephalography (EEG) was simultaneously recorded ([Fig. 1](#)). In Experiment 1, the effect
100 of discriminability between target and distractors was tested with three conditions (high, medium,
101 and low discriminability; blocked). We titrated the stimulus-onset asynchrony (SOA) for each
102 participant to ensure that their percentage of correct responses remained around 70% and to

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103 minimize task difficulty differences between conditions (mean SOA \pm SD: high = 40 ± 5 ms, medium
104 = 82 ± 13 ms, low = 271 ± 26 ms; [Fig. 1B](#)). Participants' performance across all conditions was on
105 average at 66% (SD = 6%, ranging from 55 to 85%, [Fig. 1C](#)). For the high discriminability condition,
106 average performance was at $68 \pm 8\%$, $68 \pm 9\%$ for medium, and $61 \pm 6\%$ for low discriminability. A
107 one-way repeated-measures ANOVA revealed that the percentage of correct responses in
108 Experiment 1 significantly differed between discriminability conditions ($F(1,2) = 3.73$, $p = 0.034$, η^2
109 = 0.18). Post-hoc 2-by-2 t-tests revealed that performance in the low discriminability condition was
110 significantly lower than in the high and medium discriminability conditions (high vs. low: $p < 0.01$,
111 95% Confidence Interval (CI) = [2.1, 11.9], $t(11) = 3.11$, Cohen's $d = 0.98$; medium vs. low: $p < 0.001$,
112 CI = [4.3, 10.7], $t(11) = 5.13$, Cohen's $d = 0.98$). There was no significant difference in performance
113 between the high and medium conditions ($p = 0.854$, CI = [-6.3, 5.3], $t(11) = -0.19$, Cohen's $d =$
114 -0.06).

115 In Experiment 2, the effect of set size was tested with either four or eight items presented
116 (interleaved) in the search array (medium discriminability items were used). The SOA was titrated
117 to minimize task difficulty differences between conditions (mean SOA \pm SD: 4 items = 69 ± 43 ms,
118 8 items = 129 ± 78 ms, [Fig. 1B](#)). The average performance across both conditions was at 79% (SD
119 = 4, ranging from 65 to 90 %, [Fig. 1C](#)). For the 4-items condition, average performance was at 81
120 $\pm 4\%$, and $76 \pm 5\%$ for 8 items. A two-tailed t-test showed that performance was significantly lower
121 in the 8-items condition compared to the 4-items condition ($p = 0.008$, CI = [1.7, 9.0], $t(10) = 3.27$,
122 Cohen's $d = 1.06$).

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123

124 **Figure 1. Task design and behavioral results.** (a) A button press initiated by the participant began
 125 the trial. After a random duration between 1.5 and 2.5 seconds, the search array appeared. In
 126 Experiment 1, the item shape was manipulated (blocked) to yield high (the target is a +), medium
 127 and low (the target is a T) discriminability conditions (always 4 items). In Experiment 2, the number
 128 of items was manipulated (4 or 8, interleaved; the target is always a T). The items remained
 129 onscreen for the duration of the participant's titrated SOA, immediately followed by masks, which
 130 disappeared after 500 ms from stimuli onset. After mask offset, the participant pressed a button to
 131 indicate whether the target was present or absent, ending the trial. The central fixation dot was
 132 always present. (b) Stimuli duration (SOA) for Experiment 1 (left) and Experiment 2 (right) for each
 133 condition. (c) Performance expressed as the percentage of correct responses (detecting the
 134 presence or absence of the target). Black circles represent the group average performance. Error
 135 bars represent the 95% confidence interval. Grey traces show results for individual participants.

136

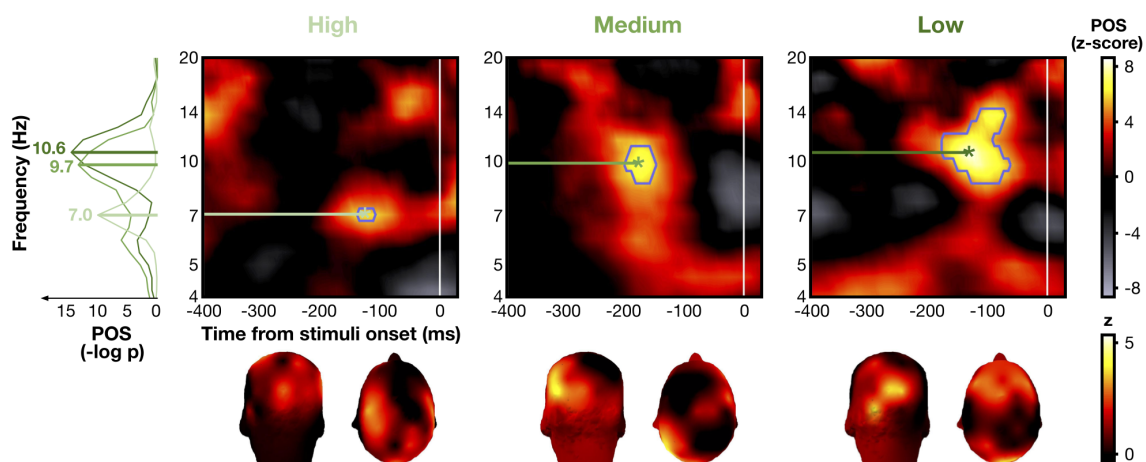
137 **Pre-stimulus phase impacts performance at increasing frequency with lower**
 138 **discriminability**

139 We first tested the prediction that the lower the discriminability, the higher the frequency of
 140 the pre-stimulus brain oscillations underlying attentional performance. Phase opposition sum (POS)
 141 [20,39,45,46] values were estimated for each frequency, pre-stimulus time point and discriminability
 142 condition in Experiment 1. A positive POS indicates that the phase is locked in correct trials and
 143 that it is locked in the opposite direction in incorrect trials (see Materials and Methods). An FDR-

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144 corrected permutation test showed a significant phase opposition between correct and incorrect
 145 trials at low frequencies (i.e., 6.6-14.3 Hz; Fig. 2) for the three discriminability conditions. We
 146 observed that the peak frequency of POS rose with difficulty: 7 Hz for high, 9.7 Hz for medium and
 147 10.6 Hz for low discriminability condition. The frequency band containing significant POS (blue
 148 outline in Fig. 2) had no overlap between the high discriminability condition (6.6 to 7.1 Hz) and the
 149 lower-discriminability conditions (medium: 8.5 to 11.1 Hz, low: 8.5 to 14.3 Hz). The topographies at
 150 POS peaks (marked by stars) showed that the effect was localized in the occipital and frontal poles
 151 (Fig. 2, bottom).

152 To ensure that the observed phase opposition effects were not spuriously generated by
 153 amplitude differences, we performed a similar analysis on amplitude. Although we observed
 154 significant differences between correct and incorrect trials (high: 8 to 12 Hz and -70 to 0 ms,
 155 medium: 6 to 17 Hz and -400 to -130 ms, low: 14 to 18 Hz at -200 ms, Fig. S1), these clusters did
 156 not overlap with those found for POS (Fig. 2); the amplitude effects differed in time and frequencies
 157 with respect to POS effects. The phase opposition effects could not be merely due to amplitude
 158 differences.



159
 160 **Figure 2. Pre-stimulus phase opposition between correct and incorrect trials in Experiment**
 161 **1. Z-score of pre-stimulus phase opposition sum (POS) of correct and incorrect trials for the high,**
 162 **medium and low discriminability conditions, combined across all electrodes and all participants.**
 163 **Blue contours indicate areas above the FDR threshold ($\alpha = 10^{-7}$, corresponding to p value**
 164 **thresholds of $2.2e-10$, $5.0e-10$, and $4.7e-9$ respectively). Stars indicate the time-frequency point of**
 165 **maximum significance (high: $z_{max} = 6.42$ at $f_{max} = 6.96$ Hz and $t_{max} = -129$ ms; medium: $z_{max} = 7.49$**
 166 **at $f_{max} = 9.75$ Hz and $t_{max} = -176$ ms; low: $z_{max} = 8.91$ at $f_{max} = 10.60$ Hz and $t_{max} = -137$ ms).**
 167 **Topomaps represent the average POS (z-score) at each electrode across participants for the point**
 168 **of maximum significance, indicated by a star. The left panel plot shows the converted POS (-log p**
 169 **values) of the high, medium and low discriminability conditions (light, medium and dark green**

170 *traces, respectively) at the timepoint with the maximum z-score (bootstrap-corrected POS in $-\log(p)$*
171 *of 10.17 for high, 13.48 for medium and 14.68 for low).*

172

173 **Post-stimulus phase-locking impacts performance only in complex searches**

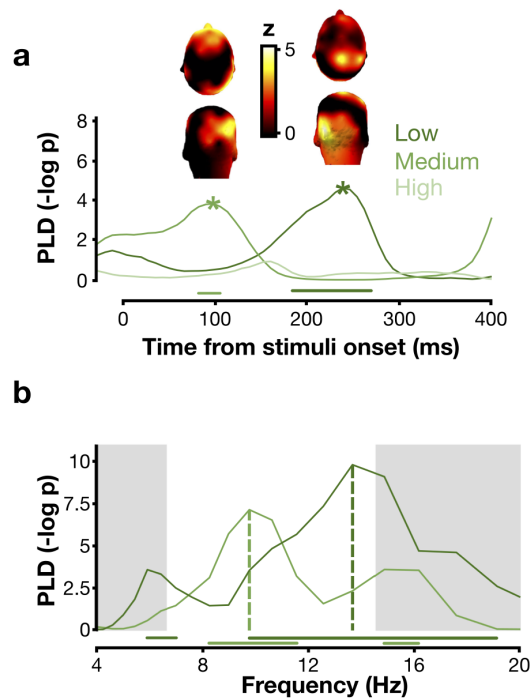
174 We tested the prediction that the lower the discriminability, the later the optimal reset of
175 neural oscillations involved in attentional search, resulting in slower post-stimulus temporal
176 dynamics. Post-stimulus phase-locking was compared between correct and incorrect trials. The
177 analysis was restricted to the task-relevant frequency band found in the pre-stimulus analysis (from
178 the lowest to the highest FDR-corrected significant frequencies, i.e., 6.6 to 14.3 Hz; [Fig. 2](#)). At each
179 time point within each participant and condition, phase-locking difference (PLD) between correct
180 and incorrect trials was averaged across the frequency band of interest. FDR-corrected permutation
181 tests showed that the PLD was significantly different from zero only in lower-discriminability
182 searches (medium: $p < 0.001$, 82 to 106 ms; low: $p < 0.01$, 184 to 270 ms), suggesting that correct
183 trials were more phase-locked than incorrect trials in these conditions ([Fig. 3A](#)). PLD was not
184 significantly different from zero in the high discriminability condition (p -values remained above the
185 FDR threshold constrained by an alpha parameter of 0.01). The topographies represent the
186 distribution of the activity at the point of maximum significance over all electrodes ([Fig. 3A](#)): fronto-
187 occipital in the medium condition, and parieto-occipital in the low discriminability condition.

188 A two-tailed paired t-test showed that the PLD peaked at significantly different latencies
189 between medium (mean \pm sd: 188 ms \pm 89 ms) and low (224 ms \pm 73 ms) discriminability conditions
190 ($p = 0.010$, 95% CI = [30,171], $t(8) = 3.28$, Cohen's $d = 1.14$; [Fig. 3A](#)). Since the latency difference
191 between average peaks (140 ms) was close to the difference in average duration of stimuli
192 presentation (SOA) for these two conditions ($\Delta_{\text{SOA}} = 190$ ms, [Fig. 1B](#)), we investigated whether the
193 PLD difference in latencies was due to the experimental design by calculating the correlation
194 between individual PLD peak latency and average stimuli duration for each participant. No
195 significant correlation was observed (medium: $r = -0.23$, $p = 0.532$, 95% CI = [-0.63,0.83]; low: $r =$
196 -0.32 , $p = 0.330$, 95% CI = [-0.85,0.52]), suggesting that the delay in PLD latencies was not likely
197 due to SOA differences.

198 If these post-stimulus phase-locking differences found here truly captured the phase reset
199 of the pre-stimulus oscillation, they should show the same frequency dissociation observed in pre-
200 stimulus activity between discriminability conditions. To test this prediction, the PLD at the timepoint
201 of maximum significance of the average traces for the lower-discriminability search conditions
202 (medium: 98 ms, low: 238 ms, stars in [Fig. 3A](#)) was plotted across frequencies ([Fig. 3B](#)). We
203 observed that the PLD peaked in a significantly higher frequency for the low discriminability task
204 than for the medium one (medium: 9.2 Hz \pm 3.0 Hz, low: 14.0 Hz \pm 3.6 Hz; paired t-test: $p = 0.009$,
205 95% CI = [1.5,8.0], $t(9) = 3.3$, Cohen's $d = 1.37$), and at similar frequencies as those observed for
206 the pre-stimulus phase opposition. Note that the high discriminability condition is not shown

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207 because no timepoint survived the FDR-corrected permutation test in the frequency-band-average
208 analysis (see [Fig. 3A](#)).



209
210 **Figure 3. Post-stimulus phase-locking difference between correct and incorrect trials in**
211 **Experiment 1. (a)** The phase-locking difference (PLD) is the difference in inter-trial phase
212 coherence (ITC) between correct and incorrect trials. The PLD curves are plotted after averaging
213 across the frequency range of the significant clusters found in pre-stimulus phase opposition (Fig.
214 2). Stars mark the timepoint of maximum significance on each trace (medium: 98 ms; low: 238 ms).
215 Topomaps represent the PLD at each electrode averaged across participants at the timepoint of
216 maximum significance. (b) PLD curves plotted at the timepoints of maximum significance against
217 frequency for the medium (light green) and low (dark green) discriminability conditions. The white
218 area indicates the frequency range of interest, taken from the pre-stimulus phase opposition effect.
219 On both panels, horizontal bars along the bottom indicate that the PLD of the corresponding curve
220 (dark green: low discriminability; light green: medium discriminability) is above the significance
221 threshold corrected for multiple comparisons (FDR).

222

223 Adding items increases the delay of the post-stimulus phase-locking effect

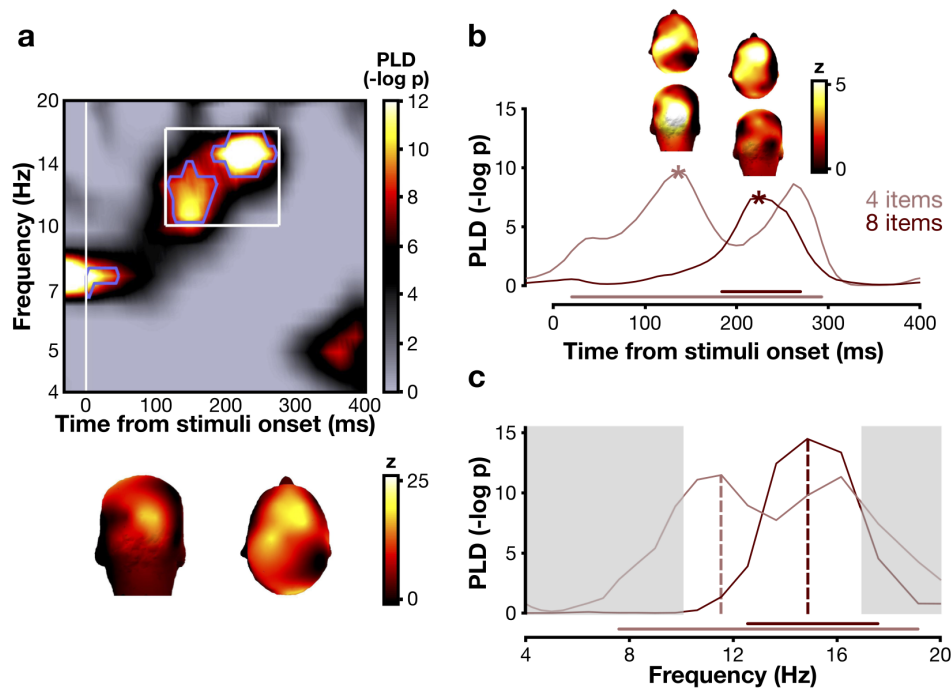
224 In Experiment 2, the number of items in the search array was manipulated (4 or 8;
225 interleaved). Since participants could not predict the set size of the upcoming trial, we did not test
226 for pre-stimulus frequency effects. Here, we specifically hypothesized that more attentional cycles
227 would be required after stimulus onset if the number of items to process increased, leading to a

228 higher frequency (for the same period of time) and/or a delayed response due to a delay in the
229 post-stimulus phase-locking. We first contrasted the post-stimulus phase-locking between correct
230 and incorrect trials for combined 4- and 8-items conditions. The FDR-corrected permutation test
231 showed that post-stimulus phase-locking value was higher in correct than incorrect trials between
232 10.2 Hz and 16.9 Hz (FDR $p < 1e-8$, [Fig. 4A](#)). The significant clusters showed a fronto-occipital
233 topographical distribution, similar to the topographies observed in Experiment 1 ([Fig. 3A](#)).

234 We then investigated this effect for each item-number condition separately. We restricted
235 this analysis to the frequency band impacting behavior by averaging the PLD between 10.2 Hz and
236 16.9 Hz. We found a significant effect of phase-locking on performance in both conditions (4 items:
237 $p < 0.01$, significant cluster from 20 to 293 ms; 8 items: $p < 0.001$, significant cluster from 184 to
238 270 ms; [Fig. 4B](#)). Critically, we observed that the 8-items condition was associated with a
239 significantly later peak than the 4-items condition (4 items: 113 ± 92 ms; 8 items: 223 ± 61 ms; two-
240 tailed paired t-test: $p = 0.030$, 95% CI = [12,190], $t(9) = 2.56$, Cohen's $d = 1.30$). As in Experiment
241 1, we calculated the correlation between stimuli duration (SOA) and peak timing to check whether
242 the timing difference could be due to the experimental design. We did not find any significant
243 correlation (4 items: $r = 0.18$, $p = 0.596$, 95% CI = [-0.62,0.80]; 8 items: $r = 0.12$, $p = 0.741$, 95% CI
244 = [-0.69, 0.80]), suggesting a dissociation between PLD latencies and SOA. The topographies taken
245 at the points of maximum significance (marked by stars on [Fig. 4B](#)) showed that the phase effect
246 is fronto-occipital in both item-number conditions.

247 Last, we investigated whether the phase-locking difference occurred at different frequencies
248 according to the item condition. We plotted the PLD at the timepoints of maximum significance (4
249 items: 137 ms; 8 items: 238 ms) against frequency for the two conditions separately ([Fig. 4C](#)).
250 Similarly as for Experiment 1 ([Fig. 3B](#)), when more items were presented, a trend toward a higher
251 frequency was apparent (4 items: $9.6 \text{ Hz} \pm 4.2 \text{ Hz}$; 8 items: $13.7 \text{ Hz} \pm 2.9 \text{ Hz}$), although this effect
252 was not significant (two-tailed paired t-test: $p = 0.12$, 95% CI = [-1.2,7.8], $t(7) = 1.75$, Cohen's $d =$
253 0.91).

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254
 255 **Figure 4. Post-stimulus phase-locking difference between correct and incorrect trials in**
 256 **Experiment 2.** (a) P value of post-stimulus phase-locking difference (PLD) between correct and
 257 incorrect trials for both conditions combined (4 and 8 items), pooled across all electrodes and all
 258 participants. Blue contours indicate areas above the FDR threshold ($\alpha = 10^{-7}$, corresponding to
 259 a p value of $4.4e-9$). The bottom topomaps represent the average activity across participants for
 260 the time-frequency area within the bounds of FDR-corrected significant blue contours (white
 261 rectangle: 114 to 277 ms and 10 to 17 Hz). (b) PLD curves plotted after averaging across the
 262 frequency range of the significant clusters found in (a). Stars mark the timepoint of maximum
 263 significance on each trace (4 items: 137 ms; 8 items: 238 ms). Topomaps represent the PLD at
 264 each electrode averaged across participants at the timepoint of maximum significance. (c) PLD
 265 curves plotted against frequency at the timepoint of maximum significance for the 4-item (pink) and
 266 8-item (red) condition. On both panels, the horizontal bars along the bottom indicate that the curves
 267 surpass the FDR threshold (correction for multiple comparisons). The white area indicates the
 268 frequency range of interest, taken from the significant PLD clusters in (a).

269

270 Discussion

271 The frequency of attentional sampling reported across the literature shows large
 272 discrepancies [4-23]. We propose that part of this heterogeneity is due to inconsistent attentional
 273 demands across tasks. The aim of this study was to investigate the link between brain oscillations

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274 and attentional demands as manipulated by the discriminability of the target and the set size in a
275 visual search task. We replicated previous findings showing that 7-10 Hz pre-stimulus phase
276 distinguishes correct from incorrect responses [20,31-40]. The novelty of the present study lies in
277 the finding that this phase opposition effect is concentrated in rising frequency with degraded
278 discriminability. This link between frequency and discriminability was also found in the post-stimulus
279 phase-locking difference between correct and incorrect search trials. A second independent dataset
280 revealed a similar pattern between the frequency of this post-stimulus phase-locking difference and
281 the number of presented items. Finally, we found significant latency effects of the post-stimulus
282 phase-locking impacting performance both when discriminability was degraded and when distractor
283 number was increased.

284 We interpret the results under the framework of hierarchical models of visual search. Most
285 theoretical accounts of attentional search propose that lower-level visual areas iteratively
286 communicate with higher-level areas (e.g., [47-50]). Top-down signaling would redirect attention
287 toward candidate items, thus amplifying specific visual neuronal populations consecutively until the
288 target is found. It has been proposed that hierarchical frameworks of visual search involving
289 iterative communication between lower- and higher-level brain regions rest on periodic neural
290 activity in these regions [5,7,20,29,30]. If the iterative communication suggested by attentional
291 search models can only process a limited number of items at each iteration, and the time allotted
292 for the search is limited (as in the current experiments), then the frequency should increase with
293 search complexity (lower discriminability or higher set size) to complete more iterations within the
294 same time window. Our results concur with this model, which constitutes the most parsimonious
295 explanation for our findings.

296 Experiment 1 shows that the less discriminable the target is among the distractors, the higher
297 the frequency of pre-stimulus phase opposition between correct and incorrect searches. This
298 suggests that the neural system can adjust to an optimal frequency, based on goal-directed
299 expectations. A similar frequency modulation was found in the post-stimulus phase-locking effect:
300 the difference in post-stimulus phase coherence between correct and incorrect responses follows
301 increasing frequency with degraded discriminability, as does the pre-stimulus phase effect. This
302 frequency increase is also observed in Experiment 2 (although without reaching the statistical
303 threshold), where trial types were interleaved (i.e., the viewer could not know in advance whether
304 they would search among 4 or 8 items). Together, these results clearly point to a direct link between
305 specific task complexity and brain oscillations. Following hierarchical models' predictions, this may
306 indicate that the more iterations are performed to find the target, the more neural cycles are
307 generated in the same constrained time window, in line with the hypothesis that more attentional
308 iterations between frontal and occipital regions are implemented through neural oscillations. Our
309 findings are consistent with a previous study, which found that the peak frequency of alpha
310 oscillations involved in a visual discrimination task decreases when the task requires temporal
311 integration relative to temporal segregation (block design) [51]. In the present study, integration

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312 could be beneficial for a partially pop-out visual task, such as the high discriminability condition (L
313 vs. +), while temporal segregation would allow processing of more demanding visual searches,
314 potentially requiring sequential processing of stimuli in the search array [52-54]. This frequency
315 modulation of pre-stimulus spontaneous oscillations may be controlled by a dynamic top-down
316 signal adjusting to task demands [7,30,51,55-57]. One can speculate that a feedback signal gives
317 rise to the lower frequency phase effect found in the high discriminability search condition, thus
318 integrating the search items and facilitating attentional capture by the salient target. A higher
319 frequency in lower-discriminability conditions could, however, enhance segregation between items
320 and contribute to their sequential processing.

321 The present results show that the phase effects are localized in both low-level (occipital) and
322 frontal regions, which is also coherent with an integration-segregation dissociation mediated by top-
323 down signals. Previous research suggests that the dorsolateral prefrontal cortex (dlPFC) facilitates
324 attentional orienting towards target-like stimuli and comparison between the currently attended
325 stimulus and the target [52,58]. Additionally, oscillations in the frontal eye fields (FEF) are involved
326 in attention shifts [8,52,58]. The theta rhythm was reported to gate and regulate the connections
327 between these anterior and posterior areas [5-7]. Coherent with these previous findings, we
328 observed that the pre-stimulus phase opposition effect is localized over frontal and occipital
329 electrodes for medium and low discriminability, whereas there is minimal frontal contribution in the
330 high discriminability search condition (Fig. 2, bottom). Moreover, the activity in occipital electrodes
331 decreases when there are more items, leaving mainly frontal activity (Fig. 4B). Together, these
332 observations suggest that frontal areas are more strongly recruited under more complex (difficult)
333 search conditions. Previous literature on exogenous (involuntary) and endogenous (voluntary)
334 attention has shown that exogenous attention relies on bottom-up signals while endogenous
335 attention relies on top-down ones [57,59-65]. Similarly, here, easier search tasks (high
336 discriminability and small set size) may preferentially involve automatic, bottom-up perceptual
337 capture, while more difficult tasks (lower discriminability or large set size) may involve top-down
338 attentional deployment. Indeed, the features that distinguish target (+) and distractors (Ls) in the
339 high discriminability condition are likely to trigger bottom-up attentional capture [66]. Bottom-up
340 signals may be supported by higher frequency bands (hardly recordable using EEG) compared to
341 top-down mechanisms, such as gamma oscillations [67,68]. This limitation can explain the absence
342 of lower-frequency effects in post-stimulus phase-locking in the highly-discriminable, partially
343 exogenous search (Fig. 3A) as well as the absence of frontal involvement in this condition (Fig. 2).
344 Our results therefore suggest that a top-down control tuning the frequency of neural oscillations
345 aids performance in difficult searches.

346 The results further show that the post-stimulus phase coherence difference between correct
347 and incorrect responses is delayed with increasing complexity (lower target discriminability or larger
348 set size). Importantly, this effect is not explained by mere differences in stimuli duration. We
349 interpret this result in the framework of two-stage hierarchical models of visual search, i.e., when

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350 search tasks are more complex, more iterations between the sensory and the attentional stages
351 are necessary, which is supported by more neural cycles. Such a mechanism implies that the
352 optimal phase reset – leading to the strongest phase-locking – will occur later on average compared
353 to less complex search tasks.

354

355 This study contributes to filling the missing experimental evidence for the current models of
356 attentional search and provides novel support for a link between brain oscillations and attentional
357 demands, which may be a factor to explain the frequency variability observed in the literature. Our
358 results suggest that brain oscillations support attentional sampling, which may correspond to the
359 iterations posited by biologically-plausible computational and cognitive models of attentional
360 search. Importantly, the pre-stimulus modulation of frequency, accompanied by post-stimulus
361 frequency and latency modulations in the same direction, indicate a capacity for low-frequency
362 oscillations (< 20 Hz) to structure the temporal dynamics of neural activity and aid top-down,
363 attentional control for maximally efficient visual processing.

364

365 **Materials and Methods**

366 **Participants**

367 Thirteen participants (6 women) were recruited for Experiment 1. One was excluded from analyses
368 because they were not able to maintain fixation. Thirteen different participants (5 women) were
369 recruited for Experiment 2. Two were excluded due to poor EEG signal quality. All participants (age
370 between 18 and 35 years) had normal or corrected-to-normal vision and declared no previous
371 history of neurological disorders or diagnoses. All participants provided written informed consent
372 and received monetary compensation for their time. The study followed the principles prescribed
373 by the declaration of Helsinki and was approved by the ethics committee "CPP Sud-Ouest et Outre-
374 Mer I," under protocol number 2009-A01087-50.

375

376 **Apparatus and Stimuli**

377 Both experiments were conducted in a dark room, with the participant sitting 57 cm away from
378 a CRT monitor (800x600 pixels; refresh rate: 140 Hz), their head positioned using a chinrest. The
379 stimuli were red letter-like symbols (oriented randomly 0°, 90°, 180° or 270° from vertical) and
380 masks (squares barred by a cross of the same size as the stimuli) presented away from a central
381 fixation dot on a uniform gray background, created under the MATLAB software (The MathWorks,
382 www.mathworks.com, version R2016b) using the Psychophysics Toolbox [69-71].

383

384 In Experiment 1, the shape of the stimuli was manipulated. Four stimuli (1.8° x 1.8° visual
385 angle) were presented simultaneously, either on the lower right or lower left quadrant of the screen
(randomly), at a fixed eccentricity (8°). In the high discriminability condition, the distractors were L
386 shapes and the target was a + shape. In the medium condition, the distractors were L shapes and

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387 the target was a T shape. In the low discriminability condition, the distractors were distorted L
388 shapes with the horizontal bar slightly shifted up so they resembled a T, and the target was a T
389 shape (Fig. 1A).

390 In Experiment 2, the set size was manipulated. The distractors were always L shapes and
391 the target a T shape. In the 4-items condition, four stimuli were presented at 8° of eccentricity (one
392 at each of the cardinal positions around fixation), and in the 8-items condition, eight stimuli were
393 presented: one at each cardinal position and one at each diagonal position around fixation (Fig.
394 1A).

395

396 **Experimental Procedure**

397 *Behavioral pre-test*

398 To assess the discriminability of items in the attentional search task for each condition, the
399 participants from Experiment 1 first performed a behavioral pre-test session testing the three
400 different stimuli shapes (L vs. +, L vs. T or distorted-L vs. T) and the two set sizes (4 or 8 items).
401 Trials in this pre-test were blocked by shape condition (104 trials per shape), with the two set sizes
402 pseudorandomly interleaved in every block (52 trials per set size in each block). Participants were
403 instructed to report as fast as possible whether the target was present or absent in the array, and
404 the stimuli stayed present on the screen until the participant pressed a response key (left arrow for
405 target present, and right arrow for absent). A t-test on median reaction times shows a weak but
406 significant difference between 4 and 8 for L vs. + items (4 items: 548 ± 46 ms, 8 items: 580 ± 48
407 ms, median ± 95% CI, $p = 0.0058$, CI = [-29,-6], $t(10) = -3.50$). There is a greater difference between
408 4 and 8 items with L vs. T (4 items: 591 ± 52 ms, 8 items: 759 ± 75 ms, median ± 95% CI, $p <$
409 0.0001 , CI = [-144,-71], $t(10) = -6.51$) and with distorted-L vs. T (4 items: 1696 ± 224 ms, 8 items:
410 2426 ± 408 ms, median ± 95% CI, $p < 0.0001$, CI = [-1208,-672], $t(10) = -7.81$). Crucially, the
411 reaction times are significantly more increased as discriminability decreases (L vs. +: Δ_{RT} median
412 ± 95% CI = 22 ± 10 ms; L vs. T: 131 ± 32 ms; distorted-L vs. T: 1052 ± 236 ms; t-test of L vs. +
413 against L vs. T: $p < 0.001$, CI = [-129,-51], $t(10) = -5.18$; L vs. + against distorted-L vs. T: $p < 0.0001$,
414 CI = [-1192,-653], $t(10) = -7.63$; L vs. T against distorted-L vs. T: $p < 0.0001$, CI = [-1089,-576],
415 $t(10) = -7.23$). We therefore label the L vs. + condition as a high discriminability condition, the L vs.
416 T as medium and the distorted-L vs. T as low discriminability. We selected the stimuli shape from
417 the medium discriminability condition (L vs. T) for Experiment 2, in which we then manipulated set
418 size.

419

420 *EEG sessions*

421 In both experiments, at each trial, participants were asked to fixate a central dot. Their eye
422 position was verified a posteriori using the electro-oculography (EOG) signal, and only trials with
423 no blink nor saccade were kept for the analyses (mean ± sd: 158 ± 50 rejected epochs). Participants
424 began each trial by pressing a key. After a random temporal jitter of 1.5 to 2.5 seconds, the stimuli

425 appeared on the screen for the duration of the Stimulus-mask Onset Asynchrony (SOA) defined for
426 each individual, and were directly followed by masks, for a total duration of 500 ms. The SOA was
427 titrated for each participant and each condition in a preliminary session with an adaptive staircase
428 procedure [72] to obtain an average performance level of 70% correct responses. The SOA was
429 re-adjusted after each block if necessary, to maintain this level throughout the experiment. The
430 average SOA across all participants was 40 ± 5 ms (SD) for the high discriminability, 82 ± 13 ms
431 for the medium, and 271 ± 26 ms for the low discriminability condition in Experiment 1; and 69 ± 43
432 ms for the 4-items condition and $129 \text{ ms} \pm 78$ for the 8-items condition in Experiment 2. The target
433 was present randomly on half of the trials. Participants were asked to report whether the target was
434 present or absent as accurately as possible, without a time limit. Participants reported the presence
435 or absence of the target using a keyboard (right arrow key for present and left arrow key for absent).
436 All participants used their right hand.

437 In Experiment 1, participants performed 6 blocks (2 of each discriminability condition) in
438 pseudorandomized order across participants, with 250 trials per block, leading to 500 trials per
439 condition in total. In Experiment 2, the set size conditions (4 items or 8 items) were pseudorandomly
440 interleaved within the blocks. Participants performed 30 blocks with 40 trials per block, leading to
441 600 trials per condition in total. The total experiment duration varied between 2 and 2.5 hours to
442 account for the EEG setup, the pre-test, the staircase procedure, and breaks.

443

444 **Behavioral analyses and statistics**

445 The behavioral dependent variable was participants' percentage of correct responses, which
446 was aimed to be maintained at 70% to ensure that participants were not guessing the answer and
447 that there was a balanced ratio of correct and incorrect trials. Trials which were rejected in EEG
448 pre-processing were also deleted from the behavioral analysis. Conditions were compared using a
449 repeated-measures one-way ANOVA in Experiment 1 (three conditions) and two-tailed t-tests
450 (post-hoc in Experiment 1).

451 In the pre-test for Experiment 1, the principal dependent variable was the reaction time
452 (measured between stimulus onset and the participant's response) as a function of the number of
453 stimuli in the search array (4 or 8). This was measured for each level of discriminability (high,
454 medium and low). Only the trials in which participants gave a correct response were included in the
455 analysis. This pre-test enabled us to compute the difference between median reaction times (Δ_{RT}
456 or slope) for 4 vs. 8 items, and thus to measure how strongly the number of distractors affected
457 performance, independently for each shape condition. The reaction times when 4 or 8 items were
458 presented, and the slopes for each shape condition, were compared using pairwise (2-by-2) t-tests.

459

460 **EEG acquisition and pre-processing**

461 EEG was recorded using a 64-electrode ActiveTwo Biosemi system. Two extra electrodes,
462 Common Mode Sense (CMS) and Driven Right Leg (DRL) were used as reference and ground.

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463 They were placed on the participant's face, with CMS on the left cheek and DRL on the right. Eye
464 movements were recorded with EOG using three additional electrodes: one on each side of the
465 eyes (to record horizontal eye movements) and one under the right eye (to record vertical
466 movements).

467 All EEG analyses were performed under MATLAB using the eeglab toolbox [73] and custom
468 scripts. Numerical computations were partly performed on the S-CAPAD platform, IPGP, France.
469 The data were downsampled to 512 Hz, re-referenced to the average over all electrodes, and
470 epoched from -1500 to +1000 ms relative to search array onset. The data were cleaned by visual
471 inspection to remove artifacts: large spurs of high-amplitude, high-frequency activity in one or more
472 electrodes (muscle contractions), blinks and saccades, as made evident by a sharp depolarization
473 and repolarization in the EOG (eye movements), slow drifts of large amplitude in more than 3
474 electrodes. In addition, electrodes were interpolated using spherical spline interpolation if they read
475 noisy signal for more than 7 % of the trials. On average, 134 ± 20 (mean \pm sd) epochs were rejected
476 per participant (~ 9 %) in Experiment 1 and 182 ± 80 epochs in Experiment 2 (~ 15 %). Epochs were
477 then labeled according to performance (correct or incorrect) for each condition.

478

479 **Phase and amplitude analyses**

480 Time-frequency decomposition was performed using Morlet wavelets on single trials [74]. The
481 wavelets' length evolved logarithmically from 3 to 6 cycles between 4 and 20 Hz. The signal was
482 expressed at every time-frequency point as a complex vector. Inter-Trial phase Coherence (ITC;
483 otherwise called phase-locking) was computed by averaging the complex exponentials over all
484 trials of a given condition for each time-frequency point, electrode and participant. This analysis
485 was done separately for correct and incorrect trials in each condition. To account for the imbalanced
486 ratio of correct/incorrect trials (70%/30%), the correct trials were randomly subsampled to attain the
487 same number as the incorrect trials (repeated 100 times).

488 To analyze whether the pre-stimulus phase between correct and incorrect trials differed,
489 Phase Opposition Sum (POS) was computed at each time-frequency point:

$$490 \text{ POS} = \text{ITC}_{\text{correct}} + \text{ITC}_{\text{incorrect}} - 2 * \text{ITC}_{\text{all}}.$$

491 A low POS indicates that the two conditions (correct and incorrect) have random phase
492 distributions, whereas a high POS means that phase-locking is strong in both conditions. The
493 measure of POS accounts for uniform distributions of phases: to ensure that the phase was truly
494 opposed between correct and incorrect trials, we checked for circular uniformity (Hodges-Ajne test)
495 of the phase angles at the point of maximum significance at sensor Oz, because it is activated in
496 the 3 conditions (high, medium and low discriminability; see [Fig. 2](#)), and ensured that no instance
497 of non-uniformity was found. Therefore, a strong phase-locking in one condition presupposes a
498 phase-locking in the other condition in opposite phase, and thus a high POS [45].

499 We also measured post-stimulus Phase-Locking Difference (PLD) between correct and
500 incorrect trials, defined as: $\text{PLD} = \text{ITC}_{\text{correct}} - \text{ITC}_{\text{incorrect}}$. A high PLD reveals a strong phase-locking

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501 for correct trials and a weak phase-locking for incorrect trials, meaning that one precise phase for
502 the reset aided performance (correct trials), and trials resetting away from this ideal phase led to
503 low performance on average (incorrect trials). As mentioned in the introduction, the term “reset” is
504 used here purely to refer to the mathematical description of the resulting signal.

505 Using the time-frequency decomposition by Morlet wavelet described above, the amplitude
506 for each time-frequency point was also computed by taking the length of each complex vector.
507 Baseline correction was applied by subtracting the mean value from -0.4 to -0.1 s from stimulus
508 onset. The same subsampling procedure as for the ITC calculation was performed.

509 The POS and PLD significance was tested using a permutation procedure. Following the null
510 hypothesis according to which there is no difference between correct and incorrect trials, we
511 compared the averaged phase-locking values to shuffled surrogates of the data within each
512 participant. The surrogates were generated by shuffling “correct” and “incorrect” trial labels while
513 keeping the original number of incorrect trials and subsampling correct trials as described above.
514 This procedure was repeated 10,000 times to obtain a null distribution. The POS and PLD were
515 converted to a z-score, by subtracting the mean of the null distribution (shuffled surrogate) from the
516 real POS or PLD, and dividing by the null distribution's standard deviation. This yielded a z-score
517 for each participant, which were then combined using the Stouffer method [45,75] to obtain a group-
518 level z-score. This z-score was expressed as a p-value using the cumulative distribution function.
519 Multiple comparisons were corrected using the False Discovery Rate (FDR) calculation with a
520 threshold α value of 10^{-7} . To test for the presence of outliers in the data, a leave-one-out procedure
521 was performed wherein one participant at a time was removed from the pool.

522 These analyses were performed from -0.4 to 0 s (around search array onset) for the POS and
523 0 to 0.4 s for the PLD. The same statistical procedure was applied to amplitude.

524

525 **Data Availability**

526 The datasets generated during and/or analyzed during the current study are available from the
527 corresponding author on reasonable request.

528

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685 **Author contributions**

686 Conceived and designed the experiments: LD, RV. Performed the experiments: LD. Analyzed the
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688 GM, LG, LD, RV.

689

690 **Additional Information**

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Supplementary material for:

Periodic attention operates faster during more complex visual search

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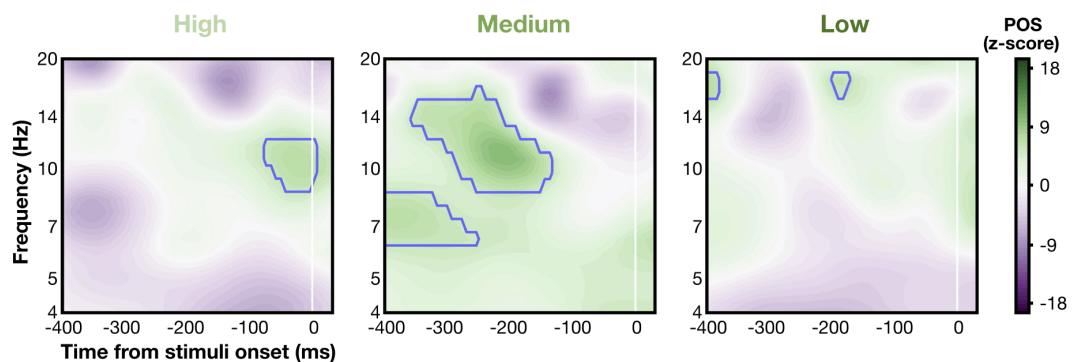


Figure S1. Pre-stimulus amplitude predicts performance in different time-frequency clusters compared to pre-stimulus phase. Z-score of pre-stimulus amplitude difference between correct and incorrect trials for the high, medium and low discriminability conditions, combined across all electrodes and all participants. Blue contours indicate areas above the FDR threshold ($\alpha = 10^{-7}$, corresponding to p values of $2.2e-9$, $1.8e-8$ and $8.2e-10$, respectively).

Complementary results

Speed-accuracy trade-off A common issue in perceptual and attentional experimentation is the tendency of certain setups to encourage speed-accuracy trade-offs, i.e., an advantage for participants to respond faster at the cost of worsened performance. Many behavioral experiments show speed-accuracy trade-offs, especially those with relatively long sessions, like those administered in our experiments. We calculated two additional behavioral measures to investigate whether our participants partook in such a trade-off. The first is the average sensitivity for each condition, as indexed by the variable d' -prime:

$$d' = |z(H) - z(FA)|$$

with d' or d' -prime the sensitivity index; $z(x)$ the function matching the z -score to its corresponding p -value (i.e., the normal inverse cumulative distribution function); H , the hit rate; and FA , the false alarm rate. For further details on hit rate and false alarms, see General Introduction Section 1.2.2. This value of d' -prime was calculated for each participant and averaged across them. The second additional measure is average reaction time.

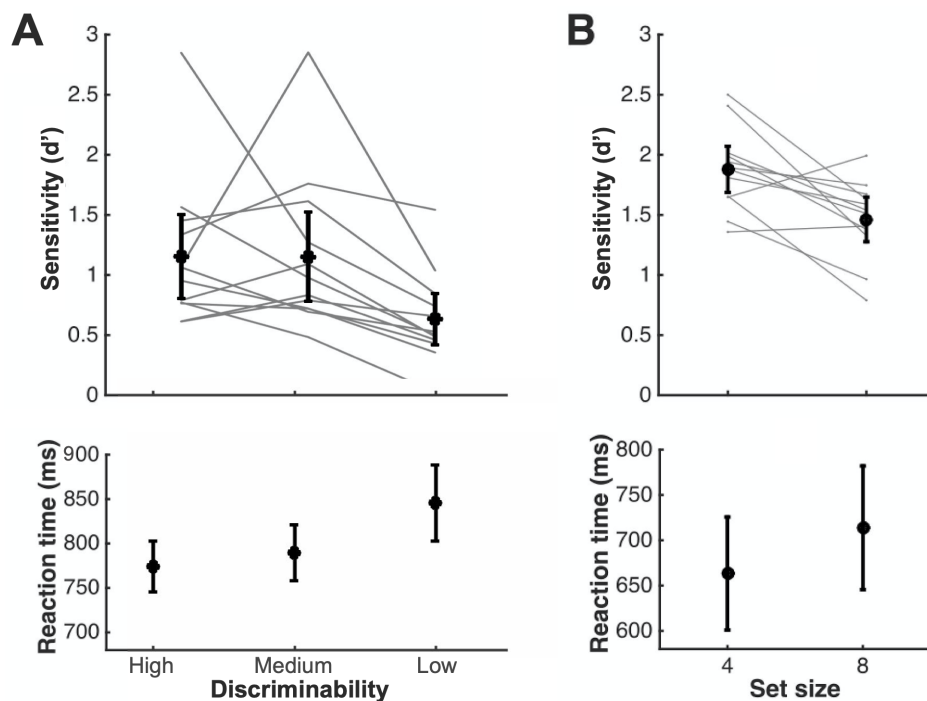


Figure II.2.1: Complementary behavioral measures. Sensitivity (top row) and reaction time (bottom row) for Experiment 1 (A) and Experiment 2 (B) reveal that participants exhibited no attentional speed-accuracy trade-off. Gray points joined by gray lines indicate individual participant results. Large black dots mark across-participant averages. Black vertical notched bars represent 95% confidence intervals.

We titrated stimulus-onset asynchrony (SOA) for each participant and each condition to match their performance levels, so we did not predict any differences in sensitivity and reaction times between conditions. d -prime was very similar between the high and medium-discriminability conditions (high average \pm sem: 1.01 ± 0.15 ; medium: 1.01 ± 0.16) but the low-discriminability condition exhibited a lower d -prime of 0.56 ± 0.09 . This relation was mirrored in reaction times (high median \pm sem: 729 ± 23 ms; medium: 753 ± 26 ms; low: 842 ± 35 ms). A repeated-measures one way analysis of variance (ANOVA) did not indicate a significant effect of discriminability on d -prime, $F(2,11) = 5.44$, $p = 0.012$, eta-squared = 33.08; but the effect on reaction time was significant, $F(2,11) = 13.63$, $p = 1e-4$, eta-squared = 55.34. Two-by-two paired-sample t -tests confirmed that the low-discriminability presentation had significantly slower responses (low vs. high: $t(11) = -4.71$, $p < 0.001$; low vs. medium: $t(11) = -4.66$, $p < 0.001$) than the medium- and high-discriminability arrays (Figure II.2.1A). Similarly, the higher set size condition exhibited significantly lower sensitivity (4 items: 1.84 ± 0.09 ; 8 items: 1.47 ± 0.10 ; $t(10) = 3.12$, $p = 0.01$) and slower reaction times (4 items: 676 ± 33 ms; 8 items: 728 ± 36 ms; $t(10) = -4.24$, $p = 0.002$) compared to the lower set size condition (Figure II.2.1B). These concurrent decreases in performance on both sensitivity and speed indicate that the decrease in the first is not due to participants rushing to answer, which would lead to faster reaction times. Thus, there is no speed-accuracy trade-off in our experiment.

Stimulus onset asynchrony As described in the article, in both experiments, the latency between phase-locking difference (PLD) peaks (Article Figures 3a and 4b) was similar to their corresponding stimulus onset asynchronies (SOAs). We ensured that SOA differences could not explain the post-stimulus latency effects by checking whether the peak timing of post-stimulus PLD effects correlated with SOA, and found that it did not.

Nonetheless, other differences between conditions, such as frequency and effect strength, may result from participants seeing the stimuli for different durations. These effects may thus reflect SOA and not, or only partially, be related to the conditions' defining differences. Future experiments of the link between neural oscillations and task complexity should, instead of adjusting the SOA, adjust task difficulty by manipulating parameters less influential on the EEG signal, such as the spatial frequency or relative contrast of classic Gabor patches.

To further test the extent of the potential effects of varying SOAs on the EEG signal in the present study, we also examined the evoked response potentials (ERPs). We did not observe an influence of the SOA on ERP temporal peaks in any participant. This favorable result complements the lack of correlation between SOA and PLD latencies, indicating that SOA differences did not affect the average EEG signal in our study.

Double peak in post-stimulus phase-locking As can be seen from Article Figure 4, the post-stimulus phase-locking difference (PLD) on 4-item trials shows two peaks over time, one at 137 ms and a later one around 275 ms after stimulus onset. Individual participant plots of PLD revealed that all but two participants exhibited such a double-peak. We suspected that this was due to two distinct types of trials, resulting in two distributions in the average across trials. In other words, on about half of the trials, participants would employ one "strategy" resulting in an early PLD peak, and on the other half, another strategy resulting in a late peak.

If participants employed a "slow" strategy on certain trials and a "fast" one on others, their reaction times should also be divided into a bimodal distribution with an early peak corresponding to "fast" trials and a late peak corresponding to "slow" trials. We thus tested the bimodality of individual participants' reaction time distributions using the Matlab function "bimodalitycoeff." However, only one participant's reaction times exhibited significant bimodality (bimodality coefficient < 0.6).

This result suggests that the double-peak observed in the 4-item PLD is not a spurious effect resulting from a bipartite strategy. Instead, it appears that strongly phase-locked activity indeed

leads to improved performance if expressed in an early and a late window within individual trials. This double-window effect may be related to the two separate time-frequency regions of significant PLD in the combined conditions (4 and 8 items) plot in Article Figure 4a (blue contours). The temporal spread of these regions corresponds approximately to that of the two PLD peaks in the 4-item condition (Figure 4B). This correspondence could tentatively indicate that a first, low-frequency oscillation exhibiting early phase-locking and a second, higher-frequency oscillation displaying late phase-locking together lead to heightened performance. However, confirming such a hypothesis will require more specific tests. Due to the task design, participants cannot indicate whether they perceived a target until the response screen appears, so they must wait to give their response. Therefore, their reaction times may not reflect their cognitive processes, as they are measured from response screen onset to keypress. We cannot reach a solid conclusion on this point but highly encourage future testing of these effects.

3 Discussion

3.1 Periodic vs. continuous cognitive sampling

We compared correct to incorrect trials meticulously in the presented article, using a statistically robust bootstrapping procedure. We also checked that the difference between these outcomes could not be explained by spurious differences (i.e., more target-absent instances or shorter SOAs in the incorrect than correct trials). We thus ensured that our separation by correct and incorrect outcomes was robustly controlled, i.e., that any other trial property was strictly the same between them. With these considerations, we have ruled out any possibility that phase and amplitude differences were spuriously related to other factors. Although our study does not demonstrate that oscillations cause worse or better performance, it has effectively shown that scalp-recorded oscillations correlate with performance on a visual search task.

As we have introduced in Section 1.3.3, the periodic sampling theory posits that visual perception and attention take temporally regular samples of the environment for further processing (VanRullen, 2016b). This theory seems to be the most parsimonious explanation for the pre-stimulus opposition in phase between correct and incorrect trials and, more generally, the link between neural rhythms and visual search performance. If cognitive sampling were perfectly continuous, we would expect the spontaneous phase of low-frequency neural rhythms not to matter for behavior. Nevertheless, we cannot exclude the possibility that an entirely separate mechanism is causing both the neural rhythmicity and the behavioral effects. In other words, the oscillations could be the result of a common cause mechanism. Indeed, such an implementation would look identical to periodic cognitive sampling. However, adding this putative third component renders the overall process more complex and thus violates the rule of parsimony. Therefore, although we cannot provide direct evidence for the cognitive sampling theory, our results indirectly support it and demonstrate that temporal oscillations correlate significantly with subtle behavioral events. Determining whether periodicity is due to perception, attention, or other processes will require precise manipulations of these functions with careful controls of any confounding interference, as we discuss in Section 3.5.

3.2 Sequential vs. parallel processing

The two-stage models of visual search that include a step of sequential, piece-by-piece processing of the array also account parsimoniously for our results. Under this view, each oscillatory cycle in the rhythms uncovered here would reflect the processing of a portion of items. However, our experiments do not test for this link, so we cannot rule out the possibility that visual search does not include any stage of sequential processing. It may be that the cycles reflect a type of "snapshot" of the whole array in parallel. Each snapshot may partially process the entire field, i.e., all items, at once (Townsend, 1990). Under this view, a single snapshot would only provide a weakly informative picture of the array. Therefore, multiple snapshots would be needed to fully resolve the search array and give a response concerning whether a target was present. This theory predicts identical processing times for target-present and target-absent trials, whereas the sequential view implies a 2:1 ratio of average processing times for target-absent and target-present trials.

Our experimental setup did not allow us to test this ratio of reaction times because participants could not respond as soon as they felt confident of the presence or absence of a target. Instead, they had to wait until the appearance of the response screen. Furthermore, they were asked to use the right hand to indicate that the target was present and the left to report its absence. This bipartite correspondence creates an additional confound in the difference between target-present and target-absent trials: any difference could be explained by handedness.

This issue extends far beyond our study alone. There is a strong divide in the community concerning whether visual search is a sequential or parallel process (VanRullen et al., 2007). Classic visual search paradigms, such as the one used in our study, cannot address this issue. Testing this dichotomy instead requires differential predictions from parallel and sequential-sampling processes, such as a cueing paradigm (VanRullen et al., 2007) or specific electrophysiological markers (Woodman & Luck, 1999). Perhaps we may imagine a new type of task in which the visual array would recreate the conditions posited by each theory. In the "sequential" condition, the items would become better resolved one after the other in sequence, whereas in the "parallel" one, they would all simultaneously gain precision at each iteration. We could then compare the behavioral outcomes of each of these setups to a classic visual search and measure which one best matches its results.

Despite these limitations, previous evidence clearly supports the sequential view over the whole-array snapshots one. This evidence comes from behavioral reports of the 2:1 target-absent to target-present reaction times ratio (Treisman & Gelade, 1980; Treisman & Paterson, 1984) and neurophysiological probing studies (Ashbridge et al., 1997; Buschman & Miller, 2009). Dugué et al. (2015b) designed an ingenious psychophysical task using visual spatial probes to test whether a difficult search was performed in sequence or in parallel. Their results strongly favor the sequential hypothesis. That is not to say that individual items are necessarily separated and strictly processed one at a time during a visual search. Gestalt experimenters have long since shown that the visual system groups objects and visual elements by properties, such as spatial proximity and similarity (Palmer, 1992; Rubin, 1958; Wertheimer, 1923). Therefore, it seems most likely that each cycle of a visual search enhances the processing of a group of items or features, rather than individual items. Indeed, our results support this view, as discussed in Section 3.6.2.

3.3 Alpha amplitude

In our study, the amplitude of oscillations in the alpha band correlated with performance (correct vs. incorrect; see Article Figure S1). This observation ties into the literature depicting the alpha rhythm as reflecting inhibition or "attentional disengagement" (see Section 3.3). However, in our experiment, increased amplitude in the high-alpha/low-beta band predicts

improved performance. This finding contradicts usual interpretations of alpha power and further confirms that neural oscillations fall into a multi-scale, complex relationship with externally observable behavior.

We also found that some participants show spontaneous, pre-stimulus alpha activity (higher amplitude than the other bands) while others display no alpha-band activity. The fact that spontaneous alpha is not observed in every individual, but seems present in approximately half of our test sample, could make it a marker. For example, it has been found that alpha power during rest is significantly higher for individuals with major depressive disorder (Jaworska et al., 2012) and likely gene disrupting mutation (LGDM), a genetic condition associated with autism spectrum disorder (Ganz et al., 2020). In neurotypical individuals, alpha power measured during the delay period in a memory task inversely correlated with fMRI BOLD signal (Meltzer et al., 2007). We will expand on these observations and discuss the overarching impact of alpha oscillations on cognition and behavior in the General Discussion, Section 1.

3.4 Phase reset

What we have termed "phase reset" in the post-stimulus phase-locking difference (PLD) effects should not be taken to mean that phase jumps such as those described by Sauseng et al. (2007) (see General Introduction Section 3.1) are taking place. If such a phase shift were occurring at the single-trial level, we should observe a significant correlation between pre- and post-stimulus frequency peaks. We wished to calculate this correlation, but this would have required reliable frequency peaks at the individual participant level, and some of our participants did not show significant peaks of frequency in the pre- or post-stimulus periods. A positive correlation would support the physical phase resetting hypothesis, but a lack of correlation does not necessarily mean that the phase reset was absent. It may mean that other effects altered the frequency relations between pre- and post-stimulus period. However, an absence of correlation may also indicate that the phase reset posited in previous reports does not correspond precisely to what Sauseng et al. (2007) describe. What authors typically report as "phase resetting" is perhaps an effect of a different nature.

Three early studies (Barry et al., 2000; Brandt, 1997; Jansen & Brandt, 1991) measured the EEG during an auditory task and separated pre-stimulus alpha activity into phase bins. They showed that the pre-stimulus phase of ongoing alpha-band oscillations significantly influenced the post-stimulus evoked response potential (ERP)'s phase. They interpret this result as supporting the oscillatory entrainment or "resetting" hypothesis of the ERP, as later described by Sauseng et al. (2007). Although this result is compatible with a trial-by-trial phase resetting of alpha oscillations, it does not test for it and cannot constitute direct evidence favoring the hypothesis. The phase of ongoing oscillations could instead influence the shape of the stimulus-induced activity by affecting the shape of an additive amplitude component.

A subsequent report (Makeig et al., 2002) claimed to test whether the ERPs observed in EEG studies were due to an additive evoked signal or to widespread phase synchronization, causing the spontaneous oscillations to appear in the average. However, their analysis method (illustrated in Figure II.3.1) seems equally inappropriate to test a potential reset. The authors defined two groups of trials, one with high alpha power and one with weak alpha power in an early post-stimulus time window (0 to 293 ms). They arranged trials according to the phase of alpha oscillations during the same time window. They claim that an uneven distribution of phases in this window favors the resetting hypothesis because it led to robust phase effects in the ERP. However, the same phase bias is also observed in the pre-stimulus period (-200 to 0 ms relative to stimulus onset), as reported in the study results and made evident by visual inspection of the sorted trials in Figure II.3.1, top panel. In other words, the post-stimulus phase follows its natural course from the pre-stimulus spontaneous oscillation, which is biased. Instead of a post-stimulus phase-resetting, the waveforms observed in the ERP can be explained

by a bias in favor of a particular phase for alpha in trials exhibiting stronger post-stimulus alpha power.

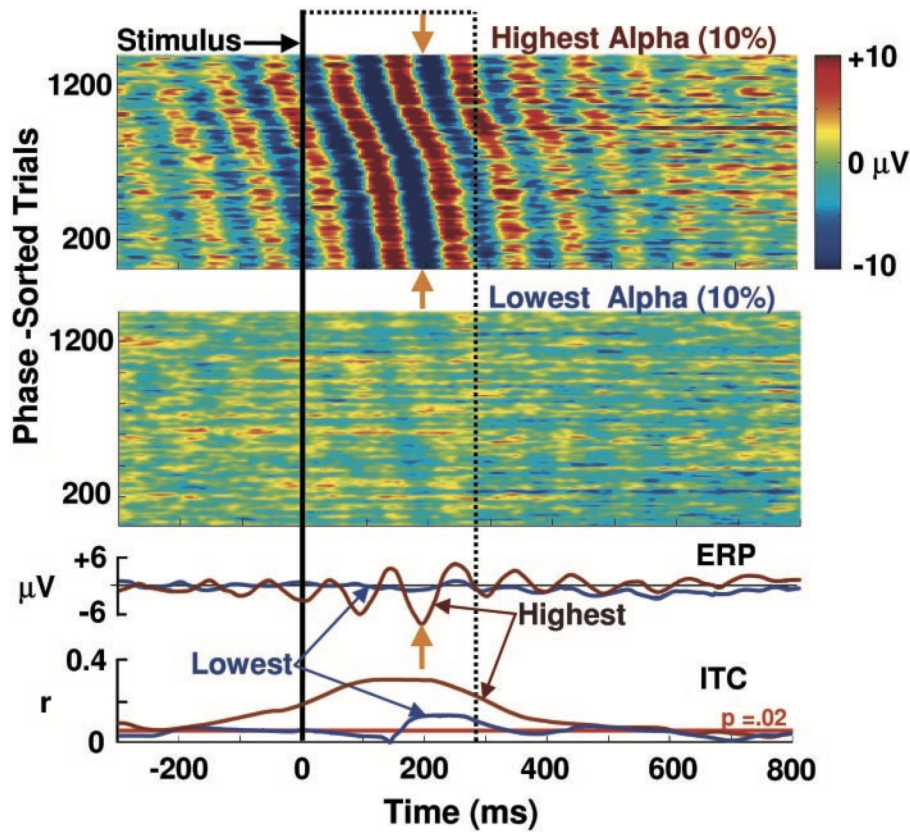


Figure II.3.1: Results reported as evidence for the phase resetting hypothesis. Each line in the two rectangular plots (top) represents a color-coded trial contributing to the evoked response potential (ERP, upper traces along the bottom of the figure). ITC, intertrial coherence. Figure reproduced from Makeig et al. (2002).

In a final example, Naruse et al. (2006) categorized their trials into subsets going from least to most seamless carry-over from pre- to post-stimulus alpha phase. They found that phasic seamlessness affects the amplitude of the P100 visual evoked potential. Once again, this relationship is compatible with but does not imply phase shifts. Similarly to Makeig et al. (2002)'s report, the increased P100 amplitude with seamless pre- to post-stimulus phase could (and indeed seems to) result simply from the oscillation progressing in a favorable phase on large-amplitude trials.

Therefore, the reader should take caution when encountering the phrasing "phase reset," as this may not correspond to the intuitive picture of single-trial phase shifts. Typically, as was done in the present study and previous ones (e.g., Dugué et al., 2015a), phase resetting is used as a description for the mathematical increase of phase coherence in post-stimulus compared to pre-stimulus periods. Dugué et al. (2015a) performed an additional analysis to check whether the post-stimulus phase depended on the pre-stimulus one. Their results do not falsify this hypothesis, but a phase dependence of post-stimulus oscillations on ongoing ones could be due to a modulation of stimulus-evoked amplitude. Thus, such dependence indirectly supports a physical phase resetting, but alternatives cannot be excluded. To date, Sauseng et al. (2007)'s physical phase resetting theory has not received sufficient evidence to rule out the classic interpretation of the ERP as resulting from an additive amplitude component, which would yield the same phase coherence results and more parsimoniously explain the short-lived duration of these effects. Further testing of this question will be needed to resolve this debate.

3.5 Limitations

3.5.1 Limitations in task design

Visual confounds We ensured that crowding would not affect task performance in our two experiments by applying sufficient center-to-center spacing between items (Pelli, 2008). Indeed, the size of stimuli leading to visual crowding effects depends on eccentricity: performance is only impaired by crowding when the stimuli fall within the same "integration field," which gets larger away from the fovea (Anton-Erxleben & Carrasco, 2013). Our stimuli lie at a sufficient eccentricity (8 degrees of visual angle) and have an appropriately small extent (1.8 degrees) to avoid crowding effects. However, the differences between 4- and 8-item conditions could still be explained by visual differences between conditions. The amount of imprints on the retina is very different between them and could drive their oscillatory effect differences.

In a future version, we can avoid this problem by making the visual array identical between conditions and changing only the instructions to the participant. In both conditions, eight items would be present on a gray background. Four of them would be white, and four of them would be black. The absolute color is indicative: we would ensure that the two colors yield identical difficulty. To interleave 4- and 8-item trials, we would present a cue at the beginning of each trial to signify either "attend only to black items," "attend only to white items," or "attend all items, both black and white." The experiment can also be blocked, giving the cue before each block only. Single-color trials would constitute the 4-item condition, and both-color trials the 8-item one. With this setup, participants would see the same stimuli across conditions. Therefore, we would be sure to be comparing differences in attentional demands and not in effects of low-level visual processing.

Additionally, the discriminability conditions also present visual differences, although the arrays are more similar in this case. As we have discussed, classic visual search setups such as those presented in our experiments are adapted to test perceptual and attentional capture. By manipulating vertical and horizontal line arrangement in this experiment, we altered the number of line terminations in our search items. Line terminations indeed constitute an important factor in visual capture (Taylor & Badcock, 1988; Wolfe & Horowitz, 2017).

We also kept the target (or the distractors) identical between the medium- and low- (or high-) discriminability conditions, respectively. With these conditions, two-by-two comparisons with the medium condition were appropriate. We ensured never to contrast high- and low-discrimination conditions directly. Nonetheless, the differences between the three conditions could be due to low-level visual processing differences. In future versions, we might use an arrangement of black and white elements as presented above, but this time at the level of the individual bars forming each item. In other words, each item would be composed of some black and some white bars, and we would instruct participants to attend only to white, only to black, or to all elements. This manipulation would ensure the arrays are visually identical between conditions and thus remove any low-level visual confound.

Symmetry In both experiments, all individual stimuli are letter-like symbols and are presented with a randomized self-rotation orientation of 0, 90, 180, or 270 degrees from vertical. For most items, this yields four versions of the stimulus. However, in Experiment 1, the high-discriminability target is a centrally symmetric "+" symbol, so turning it by a multiple of 90 degrees does not alter it. The target for all other conditions, the axially-symmetric "T," yields four different stimuli when rotated. This creates an added difference between the high-discriminability condition and the medium one, let alone the other conditions, which further differ by other factors. With this centrally symmetric target, the high-discriminability condition is not only a pop-out search by Wolfe (1998)'s definition (whereas the other two are difficult searches), but the participant also knows precisely what target shape to look for during the

blocks for this condition. In the other two conditions, the participant does not know in advance which orientation to expect for the target. Thus, we cannot know whether the effects of lower pre-stimulus frequency in phase opposition sum (POS) and lack of post-stimulus phase-locking difference (PLD) in the high-discriminability condition are genuinely due to higher ease of discriminating the target among the distractors, or instead to the absent effort of having to rotate the items mentally. We encourage future experimenters to consider these small but crucial details when designing visual stimuli and create arrangements as similar as possible across conditions, perhaps using designs like the one presented in the previous section.

3.5.2 Limitations of visual search paradigms

Visual search in its usual form cannot distinguish between attentional, perceptual, and memory effects. As we have seen, a classic manipulation in these paradigms has been to increase or reduce the number of distractors in the search array and measure the slope of reaction time as a function of set size. Researchers have been attributing these slopes to a general attentional search mechanism, but they could result from purely visual differences between the arrays. Thankfully, this does not seem to be the case. For example, searching for a red item among an array made up of blue and red items is faster than searching among the same number of only red items: we are capable of parsing the colors and searching only among the red items (Bundesen & Pedersen, 1983). Only an attentional component can explain this result. It remains that, as we have argued above, we should aim to control all other factors when studying attention, especially visual parameters. Excellent paradigms have been created to do so (Bahrami et al., 2007).

Memory tasks also exhibit significant phase effects. Phase coding (resetting and phase coherence) and local theta-band rhythms have all been described during spatial exploration and memory tasks in humans and nonhuman primates (for review see Wang, 2010). These results suggest that memory-related oscillations could be the reason for phase effects found in attentional and perceptual tasks. Our task was designed to exclude working memory components by ending trials in less than 600 ms (Silberstein et al., 2003), but shorter-term functions such as iconic memory may be at play. Experimental protocols to disentangle the contributions of these different functions are much needed. We have presented a possible way to test the effects of attention without a perceptual confound. However, removing memory effects presents a greater challenge. The working memory load is altered as soon as the number of items to search from is changed. For these reasons, classic visual search paradigms relying on the differences between set size conditions are not adapted to test attentional or perceptual effects outside of memory. To achieve this goal and to further test the distinctions between attentional sub-categories, we must turn to other frameworks, such as the Posner cueing paradigms presented in Section 1.2.3.2. We will further discuss this point in the General Discussion, Section 2.2. Visual search remains a well-adapted setup to study attentional capture and the properties of hierarchical vision.

3.6 Future directions for temporal testing

3.6.1 Delayed phase effects

In a visual search, a successful trial implies facilitation of the target and inhibition of the distractors. Therefore, the reset in the post-stimulus period could be expected to benefit performance only when the target is under attentional focus. In lower-discriminability conditions, where more attentional cycles are expected according to sequential search accounts, this would lead to a later reset. If more cycles are completed before finding the target, e.g., in a task with more items, the stimulus-triggered phase-locking effect may show a delayed peak to allow for the completion of the additional cycles. We tested this prediction by investigating the temporal dynamics of the phase-locking effect after stimulus onset. We observed that the post-stimulus

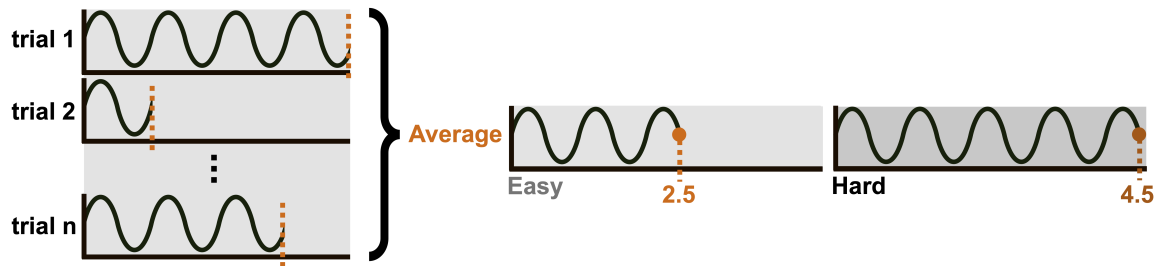


Figure II.3.2: Illustration of the new hypothesis emanating from our latency effects. In an easy task (with less items or a more easily discriminable target), less cycles are completed on average before finding the target than in a hard task, so the average effects peak later in harder tasks.

phase coherence difference between correct and incorrect responses was delayed when the target discriminability was lowered or when more items were presented. This result was obtained when modulating target discriminability and set size, suggesting a common attentional mechanism independent of task parameters. Importantly, we controlled that differences in the stimuli duration could not explain this latency effect. We propose that the completion of additional attentional cycles can explain the delay. Since the post-stimulus alpha/theta phase coherence may reflect the sensory processing of the target (Zareian et al., 2020), an increasing number of attentional cycles in less discriminable visual searches, supported by more neural cycles, implies that the phase reset will occur later on average compared to a more easily discriminable set (see Figure II.3.2). In this view, the phase reset would reflect facilitation of the sensory processing of the target rather than inhibition of distractors, thus delaying the peak of phase-locking when the target is less salient (discriminability experiment, Article Figure 3a) or embedded within a larger array (set size experiment, Article Figure 4b). Coherent with this perspective, other studies found dissociated mechanisms underlying target processing and distractor inhibition, such as independent alpha rhythms, although this issue remains debated (Mazaheri et al., 2011; Noonan et al., 2016; Wöstmann et al., 2019). This implication introduces a new hypothesis for future work.

Future testing of this novel hypothesis will be required to uncover whether latency effects truly correlate with target processing. A first possibility may take the form of simply adding targets in the more numerous search conditions. If the peak latency correlates with target processing, it should show identical values for a search with one target among four items, as in a search for two targets among eight items, because the target-to-distractor ratio is identical and the average number of completed cycles would be the same. However, if latency correlates with another parameter, such as the total number of items, the effect should still peak later in the 8-item, 2-target condition. Such a manipulation would additionally control for task difficulty. This paradigm can be taken one step further to measure the difference between an 8-item, 1-target condition, and an 8-item, 2-target one. If they are designed to be visually similar or identical, any differences between them should reflect attentional demands. With this type of paradigm, we may get closer to exposing the direct relation between neural cycles and attentional processes.

3.6.2 Cycle content

We have found increased frequency and delay for more complex search setups across our results. Higher oscillatory frequency means that the rhythmic activity accelerated, thus completing more cycles within the same amount of time. Similarly, a later average oscillatory peak in time may indicate that more cycles were carried out (see Figure II.3.2). Thus, in our paradigm, we

have an idea of the number of cycles required to perform the task, and we can relate the content of a cycle to its cognitive correlates.

Current models of visual search consider that the most plausible "unit" of iterative communication during a visual search is the feature (Deco et al., 2002; Itti & Koch, 2001; Treisman & Gelade, 1980). Intuitively, we can easily imagine that each neural cycle carries information about whole items. However, if the current models of visual search adequately represent its cognitive and neural mechanisms, then each cycle should instead carry information about more nuanced characteristics *within* each item, i.e., features. If the cycles were carrying information about whole items, they should have gotten longer in the low-discriminability condition of Experiment 1 because there is more information to process within each item (more line terminations, more difficult mental rotation). The low-discriminability condition would then exhibit a slower frequency than the high-discriminability one, but we observe the reverse: lower discriminability led to reset in a higher frequency. Therefore, in Experiment 1, the cycles do not correlate with whole items.

Furthermore, in Experiment 2, the two conditions contrast a 4-item and an 8-item array. The higher set size condition thus contains more items but also more features. Concurrent with a cycle-to-feature correspondence, the condition presenting more features also showed a higher frequency and later peak in oscillatory phase effects, i.e., a higher number of cycles.

Of course, our study was not designed to test this hypothesis and cannot provide any direct evidence for or against it. However, the results reviewed here point to a link between oscillatory neural cycles and item features. To test this hypothesis in more detail, a controlled manipulation of the number and arrangement of processed features will need to be implemented. Such experimentation may further deepen our understanding of the role of scalp-recorded oscillations in perception.

3.6.3 Replication and generalization of our results

Our study replicated the pre- and post-stimulus phase effects found by Dugué et al. (2015a) in the medium-discriminability condition. Nonetheless, the present article constitutes only a single demonstration of the effects of frequency and delay between search setups with systematically varied complexity. We have performed a first, partial replication of our results between the two experiments. The post-stimulus phase-locking effects of latency and rising frequency are found both when manipulating target discriminability and set size. These effects will need to be further replicated to ensure they do not constitute a spurious result. The global initiative EEGManyLabs (Pavlov et al., 2021) has outlined the importance of replication for electrophysiological results. Our study also calls for testing on many other search setups and using different perceptual-attentional manipulations to test whether it is a general cognitive effect or specific only to visual search. We have presented a few examples of possible future studies to address remaining open questions and the limitations of the present experiments. Another crucial follow-up will be to test whether the effects found in the present study generalize to other visual search configurations (different shape conditions, numbers of items, and other feature modulations). We hope to see results of similar tests presenting arrays with more items, less items, and with further increased or decreased discriminability in a concerted effort to create "spectra" of these properties. Such complementary tests will enable the field to fully characterize the relationship between neural rhythms and task demands.

It is interesting to note that these paradigms, whether visual search, Posner cueing, or otherwise, typically use basic visual elements, such as simple geometric shapes or low-dimensional feature stimuli. How do the results of classic visual search paradigms generalize to the real world outside the laboratory? The rare experiments using more complex, ecological stimuli are typically performed during neurophysiological recordings in nonhuman primates and push one step further, also allowing overt eye movements between the items (Bichot et al., 2015, 2005;

Zhou & Desimone, 2011). In one example with covert search, Monosov et al. (2010) report that neural activity first encodes target location (as opposed to the searched feature), perhaps indicating that saccade preparation is the priority even in the absence of eye movements. It may be interesting to test attentional capture using pictures from more familiar scenes, such as a cluttered room or a busy garden, and to measure covert and overt searches in the same settings to check if any differences are observed. The results of such experiments would be more easily generalized to everyday perceptual and attentional processing.

3.7 Scalp topography organization

3.7.1 Communication between anterior and posterior sites

The scalp topographies presented in our study (Article Figures 2, 3a, and 4a-b) show a general organization of the phase effects in two regions, one occipital and one frontoparietal. This separation across the cortical space was expected based on evidence of the visual perceptual and attentional networks presented in Sections 2.2.2 and 2.2.3. Treisman and Gelade (1980)'s model of visual search also predicted bilateral communication between occipital and anterior regions during the sequential processing stage. A transcranial magnetic stimulation (TMS) experiment (Juan & Walsh, 2003) supports this iterative communication transfer between V1 and higher-order areas in the late binding stage of visual search. These higher-order areas may be localized in parietal and frontal lobes (Foxe & Simpson, 2002). The possibility that information may not be sent directly from one to the other but through a more complex intermediate network cannot be excluded, but our results support the hypothesis of a bilateral communication between occipital and fronto-parietal regions. The most parsimonious view is one of direct transfer, which may be mediated through traveling signals at the surface of the cortex. The viability of such signals will be discussed in Chapter III.

3.7.2 Linking frequency to brain regions

In principle, the slower the rhythm, the more brain areas can be connected because the longer away the signal can travel: long-range connections take time to reach their destination, and slower rhythms allow for longer windows of opportunity (Buzsáki, 2006). It seems that more complex cognitive operations and functions (e.g., attention, consciousness, reasoning) recruit more brain areas. In other terms, there seems to be a correlation between psychological complexity and the number of areas involved. Therefore, if there were also a strong correlation between frequency and number of areas involved, as Buzsáki (2006) suggests, then more complex functions should occur in lower frequencies. However, this is in contradiction with Rosanova et al. (2009)'s report, which showed that more frontal lobes resonated at higher frequencies. Based on this experimental result, we should expect higher frequency oscillations for more complex cognitive tasks. Here, we reported phase-locking of oscillations in increasing frequency for visual searches of increased complexity. This result joins Rosanova et al. (2009)'s report in falsifying Buzsáki (2006)'s prediction. The link between oscillatory frequency and behavior can be further investigated thanks to our novel paradigm of specifically controlling the complexity of visual search setups and decomposing time-frequency dynamics in the associated neural signals.

3.8 Towards an understanding of the neural implementation of scalp-recorded oscillations

In the study presented here, we have focused primarily on the temporal dimension of oscillatory neural signals. However, as seen in the General Introduction, perception and attention have

definite spatial existence in both their cognitive effects and neural substrates. The cortical space subtending these functions has been measured with intracortical recordings and magnetic resonance imaging (MRI). As we have introduced, these tools have uncovered that a visual neuron is tuned to a specific spatial area of the visual field (Hubel & Wiesel, 1962). Neighboring neurons in the occipital cortex exhibit adjacent receptive fields (RFs) in the visual space so that overall, the physical relations in the visual field are maintained and reflected in each visual area (DeYoe et al., 1996; Engel et al., 1994; Hubel & Wiesel, 1962; Orban, 2012). It has been shown using fMRI that attention enhances the BOLD response at the cortical location corresponding to a cue's visual locus (Brefczynski & DeYoe, 1999; Liu et al., 2005; Yantis et al., 2002) or spatial orientation (Kamitani & Tong, 2005). Additionally, specific perceptual effects closely correlate with the amplitude of neural responses in corresponding retinotopic locations (Kamitani & Tong, 2005; Kastner et al., 2001; Liu et al., 2006). How do the oscillatory dynamics discussed in the present chapter interact with these effects? How are temporal oscillations implemented in the cortical space? The topographies presented in this chapter showed that the temporal oscillations involved in visual search performance are spatially spread out, recruiting frontal and occipital regions. However, EEG topographies lack the spatial precision to determine whether cortical areas were truly oscillating. For example, the effects may have been due to one deep source projecting to both poles through volume conduction. A real effort to study the spatial properties of these oscillations is needed. In order to enable this, the spatial resolution must be improved in non-invasive electrophysiological recordings. In the next chapter, we will show how we attempt to address both of these demands.

III

SPATIAL DYNAMICS

1 Background

Scalp-recorded oscillations seem to constitute an important marker of neural and cognitive functioning and have proven invaluable to inform neuroscientists about cortical architecture. We have seen how the temporal frequency of neural rhythms correlates with behavior and may rely in part on attentional demands. We will now review evidence that neural oscillatory properties are related to neuronal mechanisms. In this chapter, we delve more specifically into the link between scalp-recorded oscillations and the underlying neurophysiological mechanisms giving rise to MEEG signals.

1.1 The neurophysiological processes giving rise to MEEG oscillations

We have seen that high-frequency gamma and beta (> 20 Hz) oscillations in EEG-recorded occipital signals are a marker of core visual processing and reflect both feedback and feedforward connections. Intracortical recordings using electrocorticogram (ECoG) implants revealed that when signals are recorded at this finer scale, gamma power surges for more extended periods during the presentation of visual stimuli than those reported using EEG (Rols et al., 2001). This finding suggests that gamma power in the EEG reflects the coherent activation of more numerous or wider regions. Critically, thanks to this fine-scale resolved technology, the same authors were able to test the spatial origin of these signals. Rols et al. (2001) showed that gamma oscillations exhibited the strongest amplitude at the retinotopic location of the presented stimulus. This novel result shows that oscillatory electric signals code for the spatial location of a stimulus in the visual field.

When transcranial magnetic stimulation (TMS) is applied directly over the occipital cortex, visual neurons may show unusual activation, causing many participants to perceive illusory visual stimuli termed "phosphenes." Samaha et al. (2017) used phosphene detection as a measure of cortical excitability. They reasoned that if an identical TMS stimulation could sometimes give rise to the perception of a phosphene and other times not, then there must be a difference in the underlying state of the cortex between these two outcomes. Phosphene detection (or absence) would thus reflect an excited (or inhibited) cortex at the moment of stimulation. They found that EEG-recorded oscillations reflect this excitability: specifically, when pre-stimulus, occipital alpha or parietal beta power were high, participants tended not to report a phosphene. This result indicates that power in these frequency bands in posterior lobes mark an inhibited state of the cortex. They also found that the pre-stimulus oscillatory phase of alpha (8-14 Hz), as measured by EEG over the occipital cortex, predicted phosphene detection. This predictive effect suggests that the occipital lobe undergoes periods of alternating high and low cortical excitability of approximately 100 ms each. Interestingly, if EEG *alpha* exhibited strong power after the TMS stimulation, participants tended not to see a phosphene. By contrast, if EEG *theta* (4-7 Hz) power was elevated in these posterior regions just after the stimulation, participants usually perceived a phosphene. This chiasm in alpha and theta-band effects means that the specific frequency of oscillations arising once the activity has begun can indicate whether the cortex has entered a state of excitation or inhibition. Thus, scalp-recorded oscillations can be used to infer the state of excitability of the cortex (see also Fakche et al., 2021). Lower-frequency oscillations (4-8 Hz) seem to reflect an excitable state. In contrast, higher-frequency rhythms (8-20 Hz) may generally reflect cortical inhibition.

We have seen that a strong amplitude in gamma (> 30 Hz) rhythms combined with moderate amplitudes in low-frequency delta (< 3 Hz) and theta rhythms are markers of healthy cognitive

functioning in rats, and the reverse relation marks a very deprecated cognitive state (Llinas et al., 2007). The deprecated state and associated rhythms arise when P-type calcium channels in the thalamocortical circuit are genetically knocked out. Therefore, the oscillatory and subsequent behavioral effects appear to rely on this specific calcium channel of the thalamocortical circuit. Evidence from this study suggests that gamma rhythms are generated within the neurons connecting the thalamus to the cortex. Therefore, gamma oscillations may reflect thalamocortical activity. These findings can be linked to human studies in which the strength of 30 Hz FEF entrainment with TMS was modulated by fronto-parietal white matter volume (a marker of axon speed), suggesting that the gamma rhythm relies on these white matter connections (Quentin et al., 2015, 2016). Evidence of a direct relationship between oscillatory amplitude also comes from intracortical recordings showing that sensory neuronal spiking is increased overall when LFP alpha power is low (Haegens et al., 2011). Indeed, evidence suggests that both the thalamus (Andersen & Andersson, 1968) and neocortical pyramidal neurons (Bollimunta et al., 2011; Steriade et al., 1990) may serve as "alpha pacemakers." Bollimunta et al. (2011) recorded LFPs and multiunit activity in different layers of the primary visual cortex (V1) and showed that deep-layer pyramidal neurons oscillate in the alpha frequency independently from the thalamus. Thus, scalp-recorded alpha rhythms seem chiefly to reflect deep-layer pyramidal neuron activity, and their amplitude correlates with neuronal spiking.

Oscillatory phase also seems to play an essential role in communication between neurons, as expected from its effect on cognition and behavior (see Chapter II). Neurons in the sensory cortices were found to spike at the trough of LFP alpha oscillations (Haegens et al., 2011). Furthermore, excitatory and inhibitory neuronal synapses on neurons firing in or out of phase can enhance or suppress their activity, and thus drive temporally correlated firing between multiple cell assemblies (Engel et al., 2001; Gray, 1999; Singer, 1999). In the specific case of visual processing, when an oscillation is in place, each phase can act as a "tag" to retrieve specific components from the whole, such as features or elements of a visual object (Phillips et al., 2012).

Thus, scalp-recorded oscillations appearing in the MEEG signals seem to reflect cortical excitability, thalamocortical connections, and independent pyramidal neuron activity. Alpha oscillations constitute a marker of cortical inhibition, whereas theta rhythms indicate an excited state. The results presented in this introduction suggest that we may record and decompose signals from the human scalp to obtain instantaneous amplitude and phase in their specific frequency bands and infer neural activity. Thus, we have seen how the temporal properties of brain oscillations are extensively studied, relating them to micro-, meso- and macroscopic levels from neuronal function to cognitive behavior. However, their spatial organization remains obscure. We introduced a few general hypotheses about the spatial organization of these periodic neural signals: we now turn to this literature to identify where the field stands on the spatial dynamics of temporally oscillating signals and how we may contribute to it.

1.2 Propagating activity: the alternative hypothesis to stationary oscillations

Many models now stand to explain oscillatory recordings and their relation to micro-, meso- and macroscopic phenomena. We have seen that *stationary spatial* models depict oscillatory neural behavior as localized activity. In those cases, oscillations in distinct cerebral areas are thought to interact only through temporal (phase and power) relations: the activity itself is not thought to propagate. These stationary models can account for many reports of oscillatory coupling, phase-power interactions, and relationships between scalp-recorded activity and the individual's behavior. The imagined pattern of activation in this view resembles the "stationary bump" in Figure III.1.1b, which would essentially repeat over time to result in a strictly temporal oscillation. However, these stationary models are not the only possibility for the spatial

organization of oscillations. An alternative is *propagating* activity, such as the "traveling wave" in Figure III.1.1b. New models of *propagating* spatial activity holding strong explanatory power were developed, in complement to the *stationary* models.

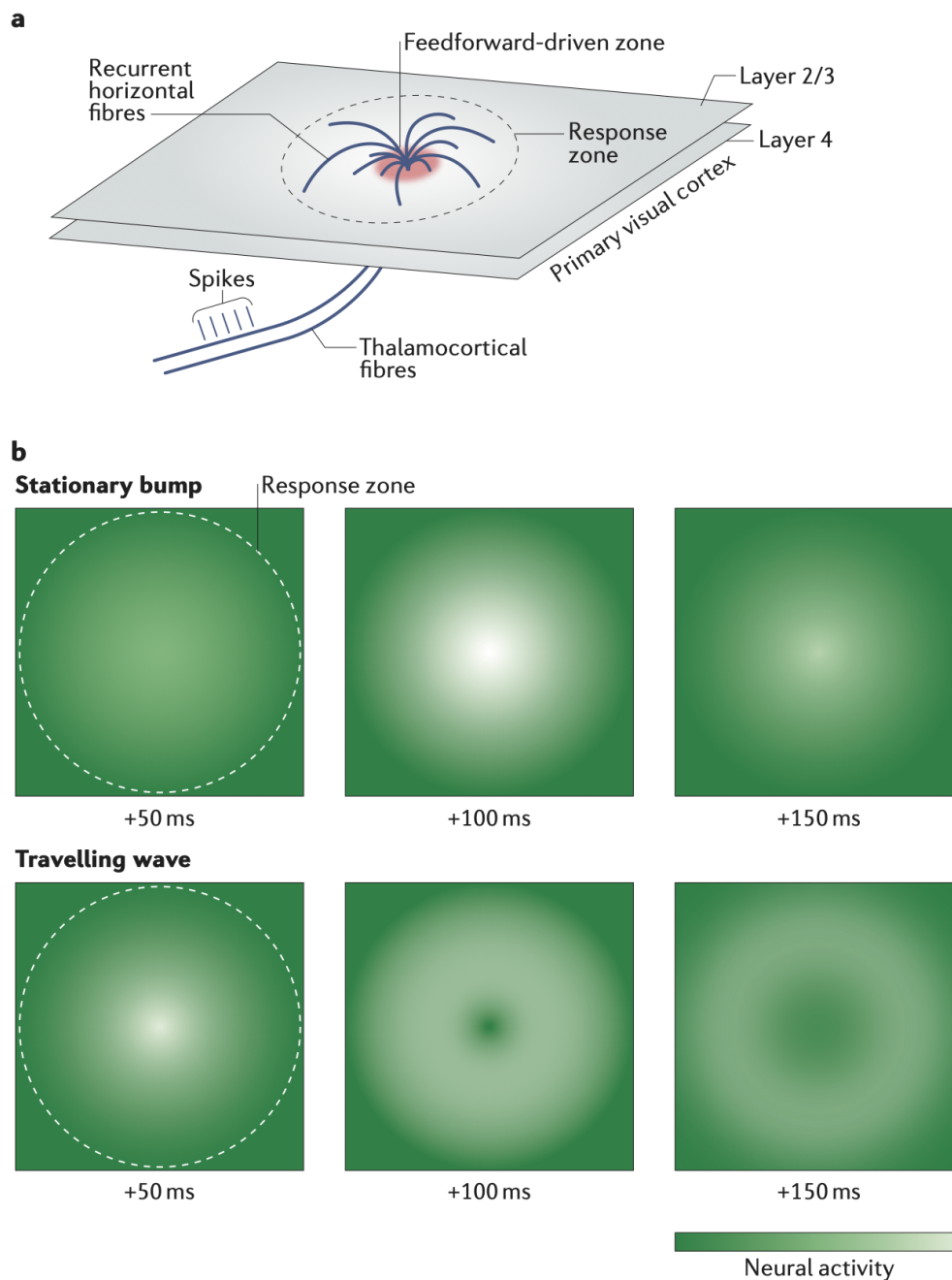


Figure III.1.1: Traveling wavefronts in the cortex. (a) Thalamocortical fibers spike upon stimulation in the visual field, which elicits a response in the primary visual cortex. Recurrent horizontal fibers carry the response activity up to 8 millimeters across the cortex surface. (b) Within this 8 mm radius, the pattern of activity may take two forms. Classically, it is proposed to produce a stationary bump (top), in which activity remains concentrated at the center. The alternative hypothesis is that the cortical response forms a traveling wave (bottom), with activity expanding outward over time and the central zone quickly returning to its initial state. Figure reproduced from Muller et al. (2018).

Neuronal conduction was found to be adequately described by traveling wave functions of time and space (Rinzel & Keller, 1973). These wave functions include both transient pulse waves (solitary fronts, like the traveling wave in Figure III.1.1b) and periodic propagation, with repeating fronts (which would form multiple rings). The predictions derived from this type of model were confirmed in manipulations of traveling waves and fronts using in vitro stimulation of rat cortex slices (Richardson et al., 2005). These manipulations show that a very short, single electric pulse (0.15 ms) delivered in one localized electrode can reliably initiate traveling waves in the cortex. It was found that layer V cortical neurons (presumably pyramidal, as they are the most numerous in this layer) are the support for the long-distance horizontal transmission of activity, and are thus necessary to traveling waves (Telfeian & Connors, 1998). These results suggest that a large simultaneous impulse arising from the collective firing of pyramidal neurons during visual stimulation (Nunez & Srinivasan, 2006) may suffice to generate a traveling wave reaching scalp electrodes. However, we cannot directly conclude whether the traveling waves observed in vitro would be large enough to be observable in MEEG.

It cannot be excluded that traveling waves in the cortex are simply an epiphenomenon arising from high inter-connection within the cortex (Muller et al., 2018). However, converging evidence of the relationship between propagating waves and brain function has put the theory of a simple epiphenomenon into question. Traveling waves mainly arise from excitatory post-synaptic potentials (EPSPs), i.e., in the activity below the threshold for sparking an action potential, as measured by local field potential (LFP) recordings and voltage-sensitive dye (VSD) imaging (for review see Sato et al., 2012), although traveling waves have also been described in action potential firing (Bringuier et al., 1999). A subthreshold modulation may serve as a mechanism to prioritize activation both in time and in space by making the spiking of specific neurons more or less likely, and thus orienting effectively to relevant locations or stimuli while selectively inhibiting others (Ermentrout & Kleinfeld, 2001; Zanos et al., 2015). Interestingly, weakly interacting or colliding wave patterns such as those observed in the neocortex could, in theory, serve as a type of code to track activation history and thus act as a local memory store (Muller et al., 2018). Similarly, single-front propagating transients may encode both stimulus location (at their center) and onset time (which can be back-calculated from the front's current location and its speed). Traveling waves were even found to link distant locations in the visual cortex and may explain the illusion of apparent motion between two stationary dots (Chemla et al., 2019), thus shaping the retinotopic representation and guiding perception.

Thus, the potential functional roles for propagating activity are numerous, and investigating this type of neural phenomenon is crucial for a true understanding of neural processes and computations. The aim of this second project is to provide tools to better characterize spatio-temporal waves by improving the precision and scale of non-invasive recording methods. We now review evidence of the functional roles of *transients*, i.e., single-front spatially propagating activity, and *periodic propagation* or *traveling oscillations*, which exhibit cyclically repeating patterns over space as well as time.

1.2.1 Single-front transients

The previous chapter showed that the literature on temporal oscillations associated with perception and attention reports many disparate frequencies. According to *stationary* hypotheses, oscillations in different temporal frequencies use phasic relations to orchestrate neuronal firing and synchrony (Fiebelkorn & Kastner, 2019). However, spatial dynamics may also play a role in these relationships. Spatio-temporal transients may coordinate the different frequencies found in the frontal and parietal cortices (Friston, 1997). Information transfers in the cortex would take the form of temporally and spatially structured patterns, which would allow efficient sensory processing. Slow horizontal connections via visual neurons' axons lead to the spreading of activation at small scales, within V1 (Chavane et al., 2000). These propagating fronts seem to

be an automatic response of the cortex to visual stimulation (Muller et al., 2014). Propagating transients can also cross large regions of the cortex spanning multiple areas (Ribary et al., 1991) and may constitute a general neural mechanism shared across the brain (Friston, 1997).

Behavioral studies have shown that attentional focus can sweep across the visual space and that these sweeps exhibit consistent speeds (Carlson et al., 2006; Kröse & Julesz, 1989; Sperling & Weichselgartner, 1995). We can speculate that these attentional sweeps across the visual field result from corresponding activation sweeps in the visual cortices. Indeed, the natural response to localized stimulation by the sensory cortices, particularly the occipital pole, seems to be the spreading of an activity pulse (Sato et al., 2012). The pulse starts from the stimulus location (i.e., its retinotopic equivalent in the visual cortex), exhibiting the highest amplitude and no delay, and expands away from it over time with decreasing amplitude at a speed of approximately 0.1 to 0.4 m/s. The traveling wavefront resulting from this spreading activity thus covers approximately 0.1 to 0.4 millimeters of cortex in 1 millisecond. Retinotopic waves traveling from the foveal representation in V4 cortex to the periphery were also found to be elicited by saccades (Zanos et al., 2015). Traveling waves have been reported in non-mammalian visual cortex (Nenadic et al., 2003) and in other, nonvisual sensory and motor cortices (Reimer et al., 2011; Wu et al., 2008). The apparent ubiquity of cortical traveling waves strongly suggests a core functional role for horizontal propagating activity.

1.2.2 Oscillatory propagation with temporal and spatial periodicity

1.2.2.1 Long-range cortical oscillatory propagation

Oscillatory traveling waves with very slow temporal frequencies (< 1 Hz) and low spatial frequencies (< 1 cycle per millimeter; one cycle typically spans the whole brain) have been reported at global scales across the cortex and may support communication between distant nodes of the default mode network, mainly observed at rest (Matsui et al., 2016), as well as task-active nodes (Majeed et al., 2011).

Long-range oscillatory waves in the theta (3-7 Hz) and alpha (8-15 Hz) bands may also coordinate the direction of information processing between different brain regions. They correlate with efficient task management and reflect perceptual events (Zhang et al., 2018). The power of high-frequency gamma oscillations, which reflect sensory neuron processing, is modulated by the phase of long-range alpha traveling waves (Bahramisharif et al., 2013). Moreover, reports show that they aid the transfer from visual occipital regions frontward (Fellinger et al., 2012; Klimesch et al., 2007a) and carry information outwards from the motor and auditory cortices (Alexander et al., 2013). Long-reaching spatial oscillations have also been found to travel in the opposite direction, from frontal to sensory lobes, and correlate with reaction time on a perceptual task (Patten et al., 2012). They may constitute one of the cortical implementations of the pre-stimulus spontaneous temporal phase effects reported in Chapter II.

Rinzel et al. (1998) modeled spatial traveling waves in a GABAergic neuronal model, showing that subtle synaptic parameter adjustments may lead to very different patterns of propagation. Similar conclusions are reached when traveling waves and pulses propagate through a chain of modeled integrate-and-fire neurons (Bressloff, 2000). The shape of spatio-temporal waves can thus reflect different underlying mechanisms and serve as signatures in electrophysiological recordings.

Thus, long-range oscillatory traveling signals may mediate communication between distant cortical areas and serve as markers of neuronal functioning. The evidence suggests that these expansive waves support maximally efficient perceptual processing with synchronized signaling leading to more rapid behavioral reactions. Indeed, perceptual regions also exhibit more localized, short-spanning spatial oscillations, which seem to enable communication and modulation within these small cortical areas. However, as we will see, their spatio-temporal dynamics are slightly more complex. We now review the link between these short-range oscillatory waves and

their associated cognitive effects.

1.2.2.2 Local spatio-temporal oscillatory waves

When a periodic signal is presented visually, the occipital pole responds with an identical-frequency resonating in the EEG called the steady-state visually evoked potential (SSVEP; Nunez and Srinivasan, 2006). This temporally oscillating response can be found in distant sources, outside the occipital lobe (Thorpe et al., 2007). Novel findings of local and long-range spatial oscillations may indicate that they are one of the main underlying components of the SSVEP. Evidence from simultaneous stimulation and recording between visual areas in the awake macaque monkey shows that alpha-band stimulation in area V4 results in LFP oscillations of the same frequency in V1 (van Kerkoerle et al., 2014). This first result supports the hypothesis that alpha oscillations travel spatially within the occipital cortex. The same study introduced an ingenious method of aligning intracortically recorded electric activity to the trough of the oscillation of interest (alpha or gamma) in the LFP trace. Over time, the direction of propagation of the signal became evident. This technique was combined with Granger causality calculations to demonstrate oscillatory propagation at a smaller scale, between the layers of V1 cortex. This latter finding proves that the cortical medium is fit to support oscillatory traveling waves. Periodic propagation has also been observed even when no periodic stimulation is administered (Gray, 1994; Roelfsema et al., 1997). These observations led us to hypothesize that local traveling waves play an important role in the spatio-temporal organization of cortical activity.

Section 1.2.1 showed that single-front transients occur naturally in the primary visual cortex (V1). Slow transients in visual cortices can be experienced and tested behaviorally during binocular rivalry (Wilson et al., 2001). Critically, these cortical traveling wavefronts become oscillatory when the visual stimulation is periodic (Sato et al., 2012). For instance, when using a periodically contrast-reversing grating in the shape of a narrow bar, mammalian V1 imaged with voltage-sensitive dyes (VSD) exhibits traveling oscillatory waves (Benucci et al., 2007). Manipulation of the retinotopic location of stimuli was associated with oscillatory waves traveling across V1 with a temporal frequency of approximately 5 Hz and propagating at speeds between 0.2 and 0.5 m/s. These reports suggest that local V1 oscillatory traveling waves may be functionally relevant.

A wave is defined as *traveling* if neighboring spatial locations (typically arranged in a line) show linear phase precession or recession in time (see Figure III.3.6 for an example). Conversely, in a *standing* wave, all spatial points exhibit the same temporal phase, but their amplitudes differ. In Benucci et al. (2007)'s report, manipulation of stimulus orientation (vertical, horizontal) correlated with cortical *standing* waves, which have also been reported in EEG recordings (Nunez et al., 2001). Spatio-temporal cortical waves may translate to equivalent spatio-temporal oscillations in the MEEG signal, but this remains to be verified. For instance, it is conceivable that *standing* waves across multiple, disparate locations of the cortex would spuriously generate *traveling* waves (phase shifts) between scalp sensors. This possibility remains to be tested.

In sum, local spatio-temporal waves are reported at multiple levels of scale in the occipital cortex. They seem to hold a functional role, particularly within V1, where their properties code for different visual functions (e.g., orientation vs. spatial tuning), and their spatial extent mediates information transfers. These local V1 waves have chiefly been investigated using finely-resolved imaging methods requiring invasive cortical probing. However, these techniques cannot be used on healthy humans. How can we link local spatio-temporal waves recorded in implanted patients and animal models to their potential equivalents in the healthy human brain?

1.3 Model-based neuroimaging

Classically, non-invasive neuroimaging of the healthy human brain has relied on the data recorded at the sensors (the electrodes placed at the scalp's surface) to infer the activity of the underlying cortical sources. Projecting source-level activity to the sensors placed outside the skull is achieved using a biophysical forward model (Kupers et al., 2020). When one aims to estimate the potential MEEG source activity, MEG and EEG sensor signals are inferred back to their spatially localized cortical sources by inverting this forward model. Thus, this classic method is dubbed "inverse modeling."

Unfortunately, inverse modeling necessarily yields an imprecise spatial estimation. There is a ratio of millions of neurons to one sensor, and it is impossible to back-calculate with precision which sources (and relations between them) gave rise to the sensor signal (von Helmholtz, 1853). This issue makes inverse modeling an ill-posed problem. It is possible to apply constraints in order to obtain a single solution (Hämäläinen & Ilmoniemi, 1994), but these constraints rely on assumptions and results in an approximation that may be quite far from the actual source activity.

Source models are needed to infer the spatial sources underlying MEEG signals (Hämäläinen et al., 1993). These source models may be used for model-based neuroimaging, in which activity is modeled in the sources and projected to the sensors using the biophysical forward model, thus removing the need for the inverse solution. Model-based neuroimaging has already proven effective in increasing the range of non-invasive neuroimaging possibilities.

Model-based intracortical neurophysiology Computational models of spatio-temporal transients already exist to describe the properties of brain slice preparation activity (Coombes, 2005). These models have been further developed in epilepsy research (Wendling et al., 2016), demonstrating that propagating transients in the cortex are computationally viable and may give rise to oscillatory signals in intracortical electrodes.

Model-based fMRI Models of traveling waves for neuroimaging have already been implemented in functional magnetic resonance imaging (fMRI) to guide and refine measures. Classically, the blood oxygenation level dependent (BOLD) signal measured in fMRI was assumed to result principally from the average of neural activity over a temporal window (Friston et al., 1995). The spatial extent of neural dynamics below the voxel scale were not taken into account.

However, new forward models simulating how neural activity gives rise to the BOLD signal suggest that the relationship between spatial cortical dynamics and resulting sensor signals is far from irrelevant (Kay et al., 2013). The data from Boynton et al. (1996) instead support the linear transform model (LTM) of fMRI. The LTM posits that the BOLD response is composed of two functions: not only a linear temporal average over the period of activation but also a non-linear spatial aggregate of local neural activity (which in turn is proportional to stimulus contrast in visual area V1). The experiments in this study were designed to falsify this hypothesis but failed to do so. This falsification failure suggests that the BOLD response is well captured by a double-aggregate of dynamic signals over space and time.

Aquino et al. (2012) also extended the simple model of linear temporal averaging by focusing on the spatial properties of cortical activity. Based on known physiological characteristics of the cortical medium, including arterial and venous flow and their relations with neuronal activity, they modeled biologically plausible hemodynamic traveling waves across the cortex. Recorded fMRI data confirms the traveling wave model's predictions. The supported propagating signals would travel at speeds between 0.01 and 0.25 m/s and remain localized, spanning up to 10 mm of the cortical surface.

Thus, model-based fMRI neuroimaging has successfully provided evidence of cortical spatial dynamics, particularly traveling waves. These techniques have been especially useful to map

spatially extended neural activity (across and between cortical areas) in higher spatial resolution techniques such as fMRI (Aquino et al., 2012; Breakspear, 2017). It can now easily be seen that model-based imaging will be of substantial help in low spatial resolution recording techniques such as EEG and MEG to understand how the currents in a folded 3-dimensional structure such as the cortex can give rise to the fluctuations we see in electric and magnetic recordings (Breakspear, 2017).

Model-based MEEG Theoretical and computational modeling have indeed informed spatial relations underlying the highly time-resolved EEG and MEG (Rajagovindan & Ding, 2011). Inverso et al. (2016) showed that retinotopy can be almost as precise using EEG as with fMRI if it is combined with modeling and supported by a structural MRI.

As we have introduced, electric waves traveling through sensors have been reported using classic MEEG imaging in the theta (Benucci et al., 2007; Giannini et al., 2018) and alpha bands (Bahramisharif et al., 2013; Halgren et al., 2019; Lozano-Soldevilla & VanRullen, 2019). Models have successfully simulated cortical activity giving rise to low-frequency oscillatory signals in the simulated MEEG sensors (Jones et al., 2009; Liley et al., 1999) and even explaining the presence of traveling signals across EEG sensors (Alamia & VanRullen, 2019). However, these accessible and efficient measuring techniques have not, to our knowledge, benefited from the modeling of spatio-temporal waves along the cortex itself. Such a model could put the fine temporal resolution of MEG-EEG to use in helping to uncover the full profile of spatio-temporal dynamics in the human cortex.

Our collaborators have developed a framework which combines an encoding model (stimulus to cortex) and a forward model (cortex to MEG sensors) to make the difference between small-scale neural synchrony and the apparent synchrony resulting from pooling over large neural populations (Kupers et al., 2020). This is a promising method to increase the interpretability of MEG and EEG because different effects of synchrony predict distinct sensor-level patterns, especially in terms of topographical organization.

Thus, a wide range of tools are already available to implement model-based neuroimaging with MEEG. It is ripe for application to oscillatory traveling waves in the human cortex.

2 Overview of the ongoing collaborative modeling project

Project leader: **Laetitia Grabot**

Contributors: **Garance Merholz, Jonathan Winawer, David Heeger**

Supervisor: **Laura Dugué**

The work performed during this thesis and presented in Section 3 of this chapter falls under an emerging collaborative research project between our team and the Center for Neural Science at New York University. Looking forward, the long-term goal of this developing collaboration is to uncover propagating oscillatory waves in the cortex using EEG or MEG recordings. To help reach this goal, our team is laying the grounds to build a methodological tool for

model-based neuroimaging based on a simple model of oscillatory spatial waves propagating along the surface of the cortex.

The spatial resolution obtained using the inverse solution alone is not sufficient to describe the spatial properties of oscillatory traveling waves within V1. As an alternative to this inverse model, we propose to model source space activity and project it into the sensor space using a forward model. If successful, our paradigm will constitute the first instance of model-based MEEG for oscillatory traveling waves and will eventually allow us to characterize the waves' exact properties. One of the main interests of such a characterization is to uncover the functional role of oscillatory propagating signals in cognition. Because knowledge on this topic is still sparse, we must first aim to characterize simple cognitive effects, such as basic perception, and work our way up to more complex psychological functions. Additionally, V1 cells respond to elementary stimuli and are most sensitive to luminosity contrast. For these reasons, the first steps of our nascent collaborative project rely on simple visual stimuli designed to probe the pyramidal cells of human area V1. The steps needed to implement, test, and generalize this new tool are outlined here to provide the reader with a roadmap of the collaborative project's methods. The specific elements which have been developed as part of this thesis (Steps 1.1, 2.1, and 3 in this roadmap) will be described in detail in the section 3.

Step 1. Predict sensor signals from modeled cortical waves

We aim to build a computational tool that will help us detect propagating waves in the human cortex. We combine a source model with a biophysical forward model to predict sensor signals (Figure III.2.1). The source model makes it simple to choose fixed parameters, so that multiple waves may be modeled. This modeled source activity is combined with a forward model projecting the cortical activity pattern to MEEG sensors.

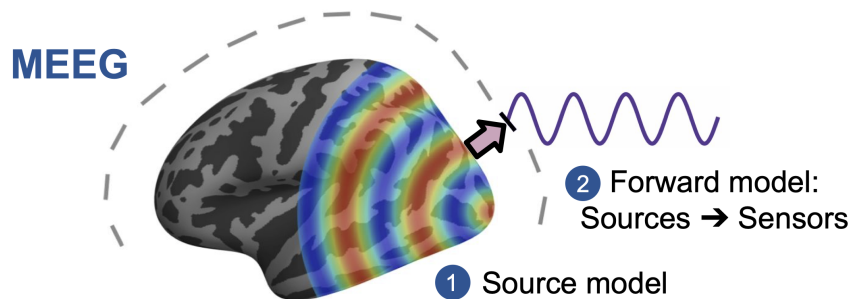


Figure III.2.1: Overview of MEEG sensor signal prediction.

Brain and cortical oscillation figure credit: Laura Dugué.

1.1. Source model The primary visual cortex (V1) is one of the easiest cortical areas to manipulate with simple, controlled stimuli and has been shown to exhibit spatio-temporal oscillatory propagation. We thus begin our exploration of traveling waves at a local level, within V1. The activity is modeled directly as electric current, in nanoAmpere (nA). The fixed parameters for the origin, direction, temporal frequency, phase, and cortical speed may all be set manually to model specific waves. Two waveform equations are implemented, a traveling and a standing one, to allow for measurements of either wave type and potential comparisons between them.

1.2. Forward model A classic forward model is used to simulate the projection of source cortical activity (taken from the previous step) out to the external EEG and MEG sensors. This forward model accounts for volume conduction through the cerebrospinal fluid, skull and scalp. It makes use of the participant's anatomical MRI for a precise representation of

the cortex (sulci and gyri), as well as the thickness of the skull and scalp, to model how the electric activity will pass through these layers. Given the source model, the forward model produces a projection of the signal obtained at each EEG and MEG sensor. These predicted signals can then be directly compared to empirically recorded EEG and MEG signals.

Step 2. Test the model projections on recorded data

We wish to compare our source model and its associated forward model projections with empirical EEG and MEG recordings. We devise a method to test our novel tool on known cortical activity displaying oscillatory propagation. We first induce waves with controlled properties in the visual cortex, so that we may later know how to detect spontaneous, uncontrolled ones.

2.1. Visual wave inducer We have seen that the visual field is projected to V1 with preserved spatial relations. This retinotopic conservation means that a wave presented in the visual field will result as a wave in V1. Thus, the first step consists in inducing waves in the cortex using visual stimulation. Thanks to fMRI retinotopic mapping, we know which point in the visual field projects to which point in V1, so we know with high precision the activity patterns occurring in V1 while we present stimuli in the visual field. By presenting visual waves, we calculate the resulting cortical waves with all their properties: their origin, direction, speed, temporal frequency, and phase. We induce two waveforms for later comparison: a traveling wave, and a standing one. All other characteristics are identical between the two waves.

2.2. Adapt the model to the induced waves We will constrain the source model to these waves which we will have forcibly induced in the cortex, i.e., we will simulate those very same cortical waves which we induced visually. Thanks to fMRI-recorded retinotopy, we can infer V1 activity. We will pass the adapted wave simulation through the forward model, to simulate the resulting EEG and MEG sensor signals. If our source and forward models are accurate, these simulated sensor signals should closely resemble the MEEG signals recorded while participants watch the visual wave inducer.

2.3. Compare source and forward model predictions with recorded data We will correlate the predicted signals with the recorded ones. Because we plan to recreate the strongest frequency component of the V1 waves which we induced visually, we expect the correlation to be strong, with the highest scores at occipital sensors and progressively lower ones away from the visual areas. We will also test the specificity of our model predictions: will the *traveling* wave prediction also correlate strongly with the signal measured when the *standing* wave-inducer stimulus is presented? If so, this may mean that the signals simply do not possess an adequate resolution for measuring such subtle cortical activations. However, if the *traveling* wave prediction only correlates with the traveling wave recorded signal, and not with the *standing* wave one, our model-based approach has a sufficiently high specificity to make the difference between two similar waveforms (all other parameters are identical). Then, our tool will constitute a very promising methodological advance for the measure of cortical traveling and standing waves. In that case, we can be quite certain that a strong correlation between prediction and actual recorded signal means that the underlying cortical activity took the shape of the modeled wave.

2.4. Generalization The final step in testing our model projections will be to compare them to spontaneous, non-induced data. The final goal is to detect spatio-temporal waves

in resting state data, in which the waves may have any point of origin, direction, phase: all properties are unknown. An intermediate step towards this goal will be to fit model parameters on task-active recordings, in which some of the parameters may be inferred. For example, a single, localized stimulus exhibiting a periodic luminosity change over time may act as a "local inducer." It would set the modeled waves' temporal frequency, and the waves' point of origin would be set to its retinotopic location. To characterize these less-defined waves, the unknown parameters (propagation speed, direction...) will be fit to the recorded data one at a time. Successive freeing and fitting of the parameters will be performed until an approximation of the waves present in the cortex is reached.

Step 3. Towards a biologically plausible implementation

We provide a simple, purely theoretical model of the physical relations in the cortex giving rise to oscillatory traveling waves. In this first computational implementation, neural populations take the form of weakly-coupled oscillators (WCOs), where each individual oscillator represents a cluster of neurons. As we will see, this version is quite artificial but adequately yields traveling oscillatory waves of the type we expect. This first implementation constitutes the lowest level of complexity for a possible biological model (i.e., simulation of the physical, cortical activity). The next level of complexity will be to build a model inspired by biological findings, i.e., rooted in neuronal mechanisms, which will include more detailed relations between neural populations or individual neurons.

3 Specific contributions from the present thesis project

We now present the three elements of this large ongoing project that were specifically developed during the course of this thesis. The first is the source model (Step 1.1), which is made as flexible as possible to allow the manual input or fitting of wave parameters. The second is the visual wave inducer paradigm (Step 2.1), designed to elicit spatio-temporal waves in V1 with known properties. The final element implemented in this project is the computational simulation of neural populations giving rise to oscillatory waves traveling across space (Step 3). This last component will constitute the basis for later developments of a biologically-based cortical model of traveling waves.

3.1 Source model

Overview The first step towards implementing a computational tool for the model-based neuroimaging of oscillatory propagating cortical signals is to build a simple mathematical simulation of these waves: the cortical source model. This first model does not intend to simulate any biological entity. It should be thought of rather as a test of whether the mathematical relations posited by the theory of cortical oscillatory propagation adequately give rise to the signals obtained in empirical data.

Thus, we start by building a mathematical model of the cortical current using simple propagating wave equations. We implement a traveling and a standing wave. Based on previous

findings of transients expanding outwards (Muller et al., 2018) and cortical waves propagating outwards from the visual cortex (Fellinger et al., 2012), we hypothesize that V1 oscillatory waves originate from the retinotopic location corresponding to the point of highest salience (or from the fovea in the absence of visual stimulation) and expand outwards.

Software To program this source model, we used the MNE Python package (Gramfort et al., 2013). This software rests on a free and open-access philosophy, making our tool accessible to all research teams once completed. It is powerful and highly adapted to our paradigm, with tools already in place to implement and visualize source and forward models. We used MNE components typically used to solve the inverse solution of estimating cortical sources from sensor data. However, we reversed this process: we manipulated the source activity to later predict its associated sensor signals.

Cortical reconstruction Our source modeling script makes use of a three-dimensional reconstruction of the cortex produced by the Freesurfer software (Dale et al., 1999). This reconstruction takes the form of a mesh, i.e., a net-like 3D structure made of vertices (points) joined by links (lines). The links and vertices form small triangular faces, which altogether recreate the surface of the participant's cortex. This cortical mesh is composed of 10,242 vertices after sub-sampling of the FreeSurfer-extracted surface. Links have equal length (3.1 mm). All cortical source locations lead to an individual forward solution by calculating the 3-layer Boundary Element Model (BEM) obtained from a sample structural MRI.

Source activity The MNE software includes functionality allowing each vertex of this cortical mesh to take on an individual value (representing electric current). We make use of this functionality to control the pattern of activity in the pericalcarine sulcus of the Freesurfer parcellation (Desikan et al., 2006), which roughly covers V1 in humans (Georgy et al., 2020). The model uses all vertices in the label by default, but for faster processing it allows further down-sampling to 25 regularly spaced sources within the label.

Waves We modeled a wave of cortical activity originating from one point and propagating outwards in every direction. The vertex corresponding to the point of origin is set manually. Our modeled wave follows the three-dimensional folds and creases of the pericalcarine sulcus such that the signal smoothly propagates along the cortical surface. In other words, if the cortex were "flattened out" or "inflated to a ball," for example, the wave would appear regular, with perfectly circular concentric rings and direct propagation from one vertex to the next.

A first algorithm calculates the cortical distance of every vertex from the origin by computing the minimum number of links lying between them and multiplying this number by the individual link length. A second algorithm passes a wave through each V1 vertex i and time point t using either the traveling wave equation,

$$A * \sin(2\pi * f_s * x_i - 2\pi * f_t * t + \phi)$$

or the standing wave equation,

$$A * \sin(2\pi * f_s * x_i + \phi) * \cos(2\pi * f_t * t)$$

where A is the amplitude in nA; f_s represents the spatial frequency in m^{-1} , which is calculated from the temporal frequency (f_t) and speed (v) as $f_s = f_t/v$; x_i is the distance in m from the wave origin vertex; and ϕ represents the phase displacement. The propagation speed, amplitude, and phase displacement are input by the user.

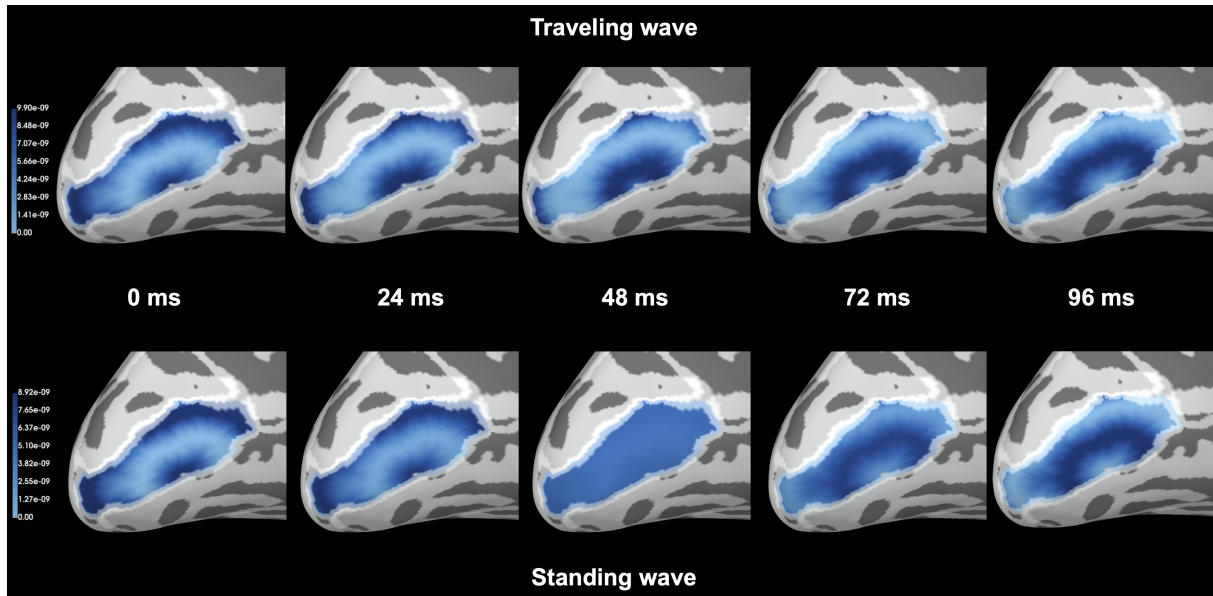


Figure III.3.1: Two instances of the source model. Over the course of 100 ms, here represented as one snapshot every 24 ms, a traveling wave (top) propagates outwards from the origin (gray point), whereas a standing wave (bottom) with otherwise identical parameters undergoes a pattern reversal. The left cerebral hemisphere is represented with the "inflated" setting to view gyri (light gray) and sulci (dark gray). The viewing angle is set to the posterior portion, looking into the sagittal cut between the two hemispheres. The semi-transparent white outlines delimit the cortical parcellation, with the source activity (light to dark blue) constrained to the pericalcarine sulcus (V1). In this example, the wave origin is set to a ventral vertex. The amplitude is set to 1 nA. The speed is set to 0.1 m/s and the temporal frequency to 5 Hz, yielding a spatial frequency of 50 m^{-1} . Cortical images were rendered using the MNE-Python toolbox, function `mne.SourceEstimate.plot`.

Native MNE tools allow for the visualization of our simulated cortical waves, as is illustrated in Figure III.3.1. The traveling wave equation cycles through vertices according to their distance from the origin. Therefore, the wave travels outwards from the center in all directions. This creates the desired circular pattern. The direction can easily be reversed by inverting the distance values associated with each vertex, for example. A similar algorithm for calculating distance as the one presented here can also be used to change the shape of propagation for future adaptations, e.g., to implement linear waves.

Preliminary use of the forward model It has been proposed that spatially traveling waves in sensor activity may result from cortical standing waves. Standing waves in V1 would yield phase shifts at the level of the sensors due to volume conduction. To begin addressing this possibility, we generated preliminary, noiseless versions of our source and forward models. The source models depicted in Figure III.3.1 were passed as input to the forward model, which takes volume conduction into account, to project a standing and a traveling wave outwards to the sensors. Our simulation results show that a cortical standing wave does not induce phase advancements in the sensors, neither MEG nor EEG (see Figure III.3.2, right). Only a cortical traveling wave induces phase shifts across the sensors (Figure III.3.2, left). If the classic forward model used here accurately describes the projection from sources to sensors, this result suggests that volume conduction alone does not produce phase precession or recession.

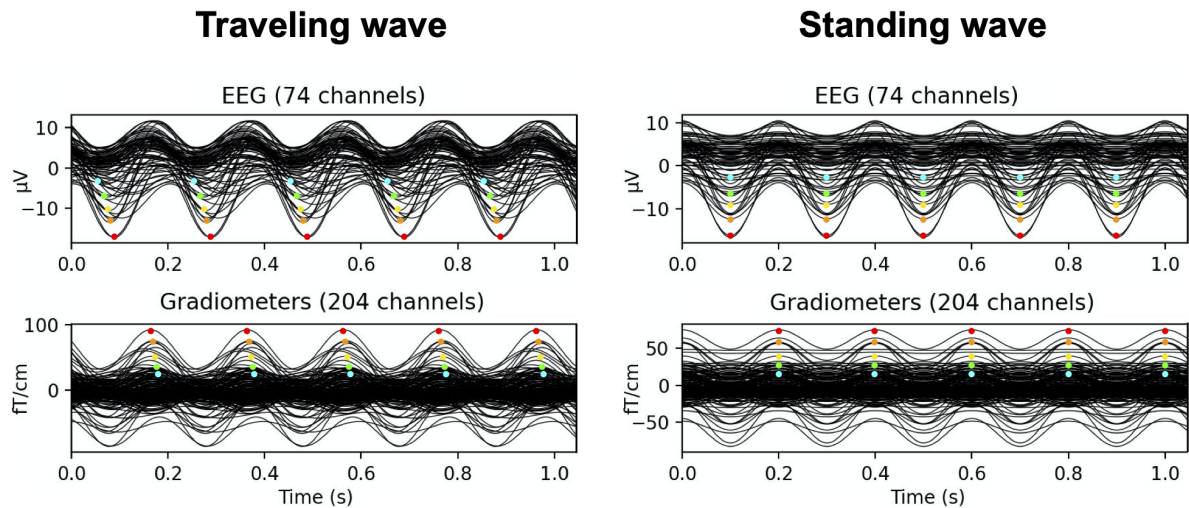


Figure III.3.2: Modeled standing waves do not elicit phase shifts between sensors. The two source models presented in Figure III.3.1 are projected onto EEG sensors (top) and MEG gradiometers (bottom) using the biophysical forward model. Each black line represents a sensor. As indicated by the phase markers (colorful dots), a traveling wave (left) yields phase shifts in EEG and MEG sensors, whereas a standing wave (right) produces sensor signals that are strictly in-phase. For MEG, only gradiometer projections are shown, but similar results are obtained in magnetometers.

3.2 Visual wave inducer

Now that we have constructed a complete simulation of the cortical traveling waves, we wish to measure its performance in predicting empirical sensor data. Such a test requires a precise hypothesis of the waves present at the cortical surface. We elected to induce cortical waves ourselves. The present section describes how we induced traveling and standing waves in V1 using the Visual wave inducer.

3.2.1 Wave inducer methods

The purpose of the Visual wave inducer is, as its name indicates, to induce traveling waves and standing waves in visual areas with known properties using a visual stimulus. We aim to make the waves as close as possible to what was observed in the literature. Therefore, we wish to induce oscillatory waves expanding outwards from one retinotopic location at a speed of 0.1 m/s. We have seen that traveling waves are observed in the theta range, which matches the low-frequency cognitive rhythms associated with perception and attention. We also wish our participants to remain comfortable while viewing the stimulus, i.e., not to experience fatigue and migraines from high-frequency flashes. For these combined reasons, we set the temporal frequency of our visual inducer to 5 Hz, as has been reported in local traveling signals previously (see Section 1.2.2.2). We thus programmed the traveling wave stimulus so that every point on the screen oscillates at 5 Hz, resulting in the same temporal frequency oscillation in V1.

Stimuli V1 is sensitive to luminosity, so we use the screen luminance to manipulate activity in the visual cortex. The wave inducer code was written using the MatLab programming software (The MathWorks, www.mathworks.com, version R2016b). Each pixel on the screen is controlled via a Psychophysics Toolbox fullscreen window (Brainard, 1997; Kleiner et al., 2007; Pelli, 1997). Once again, to avoid discomfort while viewing the stimuli, the maximum stimulus luminance

is set to 75% of the maximal screen luminance. The minimum is set to 25%. These luminance values minimize strong flashing in the darkened experimental MEG room. Participants will view the inducer on the screen present in this room, which is 44.2 cm tall by 79.6 cm wide and stands 76 cm from the participant's eye. With these measurements, the stimuli's onscreen sizes can be precisely calculated to obtain the required degrees of visual angle during viewing.

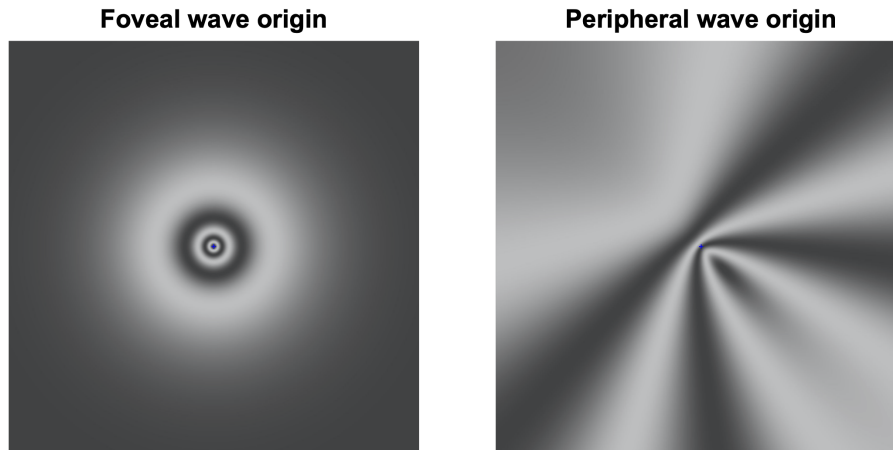


Figure III.3.3: Single-frame examples of the onscreen Visual wave inducer. The wave exhibits higher spatial frequency (thinner rings) around the central fixation point (marked by a small blue dot) to account for cortical magnification. In the traveling wave condition, the luminance bands expand outwards from the wave origin; in the standing wave condition, the stimulus undergoes a pattern reversal. These dynamics are designed to elicit the source activity patterns illustrated in Figure III.3.1.

We wish to induce cortical waves with fixed properties. Specifically, the cortex should exhibit regular patterns of activity, with a simple circular sinusoidal yielding equally spaced bands, as in our source model (see Figure III.3.1). However, the fovea is overrepresented in the cortex, whereas the periphery is underrepresented. When creating our stimulus, we must take this central magnification and peripheral reduction into account: more information must be presented around the fixation point and gradually decrease towards the periphery. This transformation is achieved by applying an M scaling function to each visual field location with this equation taken from Strasburger et al. (2011):

$$E_{cort} = M_0 * E_{vis} / (E_{vis} + E_2)$$

with the magnification value $M_0 = 17.3 \text{ mm.deg}^{-1}$ and intercept factor $E_2 = 0.75$ from Horton and Hoyt (1991). Each spatial location (pixel) is transformed based on its eccentricity E_{vis} (distance from the fixation point) in degrees of visual angle. The resulting corresponding cortical eccentricity E_{cort} is in mm.

The cortical magnification transformation thus relates every pixel to its location on the V1 cortex surface. It is then possible to create any desired image on the cortex surface, and it will appropriately distort it on the visual screen to ensure it gets projected as desired. In the example of our visual inducer, the circular waves can thus start from any point of origin, not only the center. An illustration of peripheral-originating waves in the visual inducer is given on the right panel in Figure III.3.3.

We introduced two visualization conditions: full-field and quadrant (Figure III.3.4). In the full-field condition, the stimulus covers the whole screen. However, in the full-field condition, the stimulation will project to both halves of the visual field simultaneously, so V1 in both hemispheres will activate together and likely lead to oscillatory interference. Thus, in the

quadrant condition, the stimulus is presented only in the lower-right portion of the screen, with diagonal borders to avoid stimulation on the vertical and horizontal meridians. This way, the stimulus falls below the horizontal meridian: this has been shown to elicit more robust MEG responses (Portin et al., 1999), and it avoids recruiting dipoles on opposite banks of the pericalcarine sulcus, which may cancel out. Thanks to the additional visual field restriction to the right of the vertical meridian, only the left-hemisphere V1 will exhibit oscillations, thus minimizing interference and dipole cancellation. Thus, this quadrant condition will allow us to test the direct relation between cortical oscillatory waves and MEEG sensor-level signals. However, the full-field condition is also crucial to characterize the contributions of opposing dipoles to the signals recorded all over the scalp. Indeed, such cancellation may mask the signal at the occipital sensors directly above the opposing dipoles. However, the activity may surface at other locations, for example. The Visual wave inducer will enable us to test such possibilities.

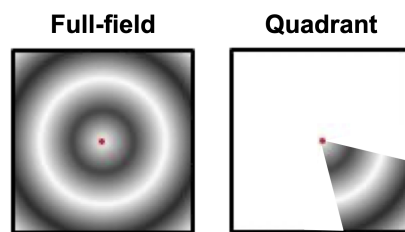


Figure III.3.4: Illustration of the full-field and quadrant conditions of the Visual wave inducer. In the full-field condition, the visual wave stimuli cover the whole screen. In the quadrant condition, only a portion of the bottom right quadrant exhibit wave stimulation, and the rest of the screen is blank.

Experimental session design The experimental session is cut into trials, runs, and blocks. One trial consists of 2 seconds of stimulation using the wave inducer. Trials are separated in time by 2-second blank screens. A *run* is composed of 8 successive trials, half of which are traveling waves and the other half standing waves, pseudorandomly ordered. A period of 12 seconds separates two successive runs. Finally, one *block* is composed of 8 *runs*. All trials in a block have the same visualization condition, full-field or quadrant. A total of 14 blocks is administered in one experimental session, with 7 full-field and 7 quadrant blocks pseudorandomly interleaved. Optional breaks are offered to the participant after each block and may last up to 3 minutes, for a total session duration of approximately 2 hours. With this experimental design, each combination of conditions (traveling or standing wave, with full-field or quadrant visualization) is repeated in 224 individual trials.

In order to minimize saccades and microsaccades, which significantly affect electrophysiological signals, participants perform a task at fixation, and an eye-tracker is used. If the participant breaks fixation from the central dot, that trial is repeated at the end of the block.

The task at fixation consists in detecting whether the color of the fixation dot briefly changes at any moment during the run. The target fixation-dot change is pseudorandomly assigned to 25% of trials (~1 to 3 targets out of the 8 repetitions constituting a run, drawn from a uniform distribution). The color change occurs 0.5 to 1.8 s after the start of each trial: this delay is also pseudorandomly drawn from a uniform distribution. The color change lasts only 150 ms, after which the fixation dot returns to its original color, making it a difficult detection task requiring focus. The change never occurs on the first trial in a run so that attention is maximized throughout the run. We checked the timings of all our stimuli using a photodiode and oscilloscope.

Planned data collection For the purposes of reproducibility and testing over the population of healthy, neurotypical individuals, we plan to recruit right-handed participants with normal

or corrected vision and no history of neurological and psychiatric conditions. Only participants without certain implanted metals can run in the MEG to yield a reliable signal. In our project, we will record simultaneous EEG and MEG because the virtues of doing so are multifold:

- Internal replication: the data obtained from the MEG serves as a test for the data from EEG recording and vice-versa. We may check whether our results are replicated from one recording technique to the next.
- Large amount of data: EEG and MEG do not capture the same sources (e.g., gyral and sulcal activity). We can inform one measure with the other. The added data allows for higher precision.
- Compare model fits and estimations between MEG and EEG to improve EEG estimations (methodological guide): EEG is cheaper and easier to use and implement, so it is useful to improve its precision, making informative data accessible to more scientists.

Thanks to this novel experimental tool, we will induce spatio-temporal oscillatory waves in the V1 cortex of healthy, human participants. We will know with precision the parameters of these waves. With our help, Laetitia Grabot (project leader) has begun to run the visual wave inducer paradigm in the MEG with concurrent EEG. Data collection is currently ongoing.

The next step will be to simulate these exact waves in our source model (previous section), predict their resulting theoretical MEEG signals using the classic forward model, and compare those predicted signals with the empirical signals recorded during wave inducer visualization. Suppose the model-predicted traveling signal correlates significantly with the empirical traveling signal but not with the standing one. In that case, our first model-based approach will be sensitive and specific enough to make the difference between otherwise identical traveling and standing cortical waves. This positive result would constitute solid grounds to explore non-induced data and attempt to uncover propagating signals using our new tool.

3.3 Towards a biologically plausible implementation

As we have mentioned, the source model presented in Section 3.1 does not represent any biological entity directly. The activity in the cortex is measured in theoretical Amperes, i.e., in units of current arising from electrical dipoles. These currents give rise to the EEG and MEG signals via electric and magnetic conduction, respectively. This theoretical cortical activity is many steps removed from the underlying neural mechanisms giving rise to spatio-temporal oscillatory dynamics. In order to fully understand cortical propagating waves, we will need a biologically-based account of their emergence. Such a complete description is beyond the scope of this thesis, but we propose an intermediate account based on physics rather than biology. Indeed, the physical relations connecting nodes in a network of Weakly Coupled Oscillators (WCOs) may constitute a first step towards understanding the neural underpinnings of scalp-recorded oscillations. A theoretical implementation of WCOs has successfully simulated oscillatory synchrony in the monkey V1. Modeling the cortex in this way reproduces the temporal dynamics found in empirical recordings under various conditions (Lowet et al., 2017). WCOs have also been found to give rise to inter-oscillator traveling waves when they followed linear frequency gradients (Zhang et al., 2018, Figure III.3.5).

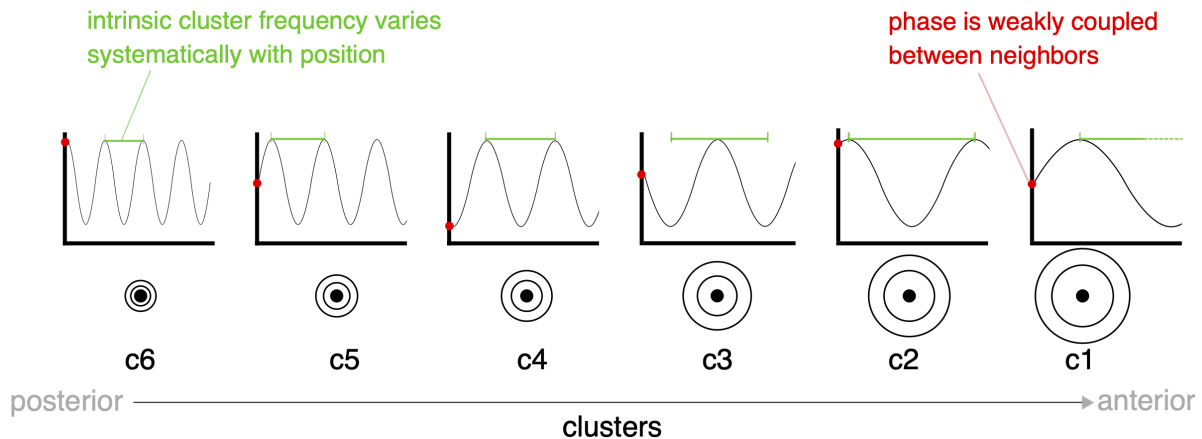


Figure III.3.5: Properties of WCOs. Weakly coupled oscillators (WCOs) must exhibit two properties to give rise to traveling waves (Ermentrout & Kopell, 1984; Zhang et al., 2018). The intrinsic frequency displayed at each cluster must increase or decrease linearly according to spatial location (notice that the green bar representing the oscillatory period becomes longer towards anterior clusters). The second necessary property is their phase relationship: the phase of each cluster must depend on those of its neighbors but not be fully determined by them (Kuramoto, 1981). Here, c1 through c6 represent six oscillating clusters arranged from posterior to anterior regions (bottom) and associated with their intrinsic time courses of activity (top).

Mathematical equations controlling the individual phases of local oscillators closely approximate the global oscillatory activity displayed by neural networks (Schwemmer & Lewis, 2012). Indeed, adjacent locations in a physical medium, here the visual cortex, will synchronize after a delay and exhibit a small phase shift if they are connected via phasic interdependence (weakly coupled; Ermentrout and Kleinfeld, 2001). We may picture the oscillators modeled here as clusters of neurons dwelling physically close to each other (Figure III.3.6, center) with each cluster acting as one large dipole, thus outputting electric activity. Each cluster oscillates locally at its intrinsic frequency. The clusters are "weakly coupled" because the phase at any cluster depends on the phases displayed by its neighboring clusters, but their influence is low. This minimal influence means that no substantial changes will occur over short time periods (e.g., within only a few oscillatory cycles of each cluster). However, given a sufficient delay, the oscillators are found to synchronize to the same frequency and show phase alignment (Schwemmer & Lewis, 2012).

We have implemented a simple network of weakly coupled neuron populations using the MatLab software.

Before launching the simulation, we set the free parameters. Ten nodes represent ten neuronal populations. The variable ϵ represents the strength of the coupling between neighboring nodes and is set to 20%. The total time for the simulation is given 10 seconds, enough to reach a stable state (> 4 s). Δt is the time step and is set to 1 ms for a total of 10,000 time points. ω_i is the intrinsic frequency of each oscillating cluster i . The intrinsic frequencies range from 1 to 9 Hz so that they average to 5 Hz. A random starting phase $\theta_{0,i}$ is assigned at each cluster.

Once the simulation has started, the following algorithm loops over each time-step. All nodes are connected to their two direct neighbors. The end nodes ($i = 1$ and $i = 10$) only have one neighbor, so these are separated from the other clusters to make them connect with their only neighbor. However, the logic remains the same for all clusters. A new phase is set at each time point t for each cluster i , by calculating the change in phase $\Delta\theta$ and summing it with the

phase at the previous time point:

$$\theta_t = \theta_{t-1} + \Delta\theta$$

where $\Delta\theta$ is calculated as the phase shift for the intrinsic frequency of the present cluster added to the sine of the difference in phases with the neighboring clusters. This coupling is weakly weighted by multiplying with ϵ :

$$\Delta\theta = \Delta t \left(\frac{\omega_i}{2\pi} + \epsilon (\sin(\theta_{i-1,t-1} - \theta_{i,t-1}) + \sin(\theta_{i+1,t-1} - \theta_{i,t-1})) \right)$$

Thus, the simulation produces the resulting phases at each cluster over all 10,000 time points in the 10 second period.

We have executed this simulation and plotted the output for six of the ten clusters after 9 seconds of weak coupling between the 10 clusters, illustrated over a period of 1000 ms in Figure III.3.6. As can be seen, there is a phase gradient across space (the peaks of neighboring cluster oscillations happen one after the other in physical order), and five cycles are completed in one second, corresponding to a 5 Hz oscillation.

The simple WCO model presented here gives us an idea of the mathematical relationships between adjacent cortical locations that may give rise to cortical traveling waves. The next step in uncovering the neural mechanisms leading to oscillatory propagation will be to model biological entities displaying these activity patterns and connections, e.g., via axonal connections. This latter implementation is not further discussed in this thesis as it will be addressed in later work.

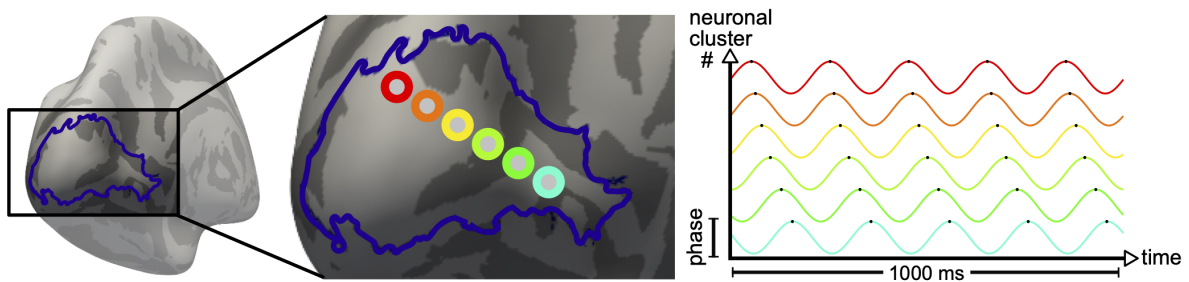


Figure III.3.6: Weakly coupled oscillators exhibit traveling waves. The time courses on the right represent the activity over a one-second period in six modeled clusters after 9 seconds of weak coupling. For each cluster, five cycles are completed: at time 0 (not shown), each cluster was oscillating at its intrinsic frequency, but after weak coupling, all clusters synchronize to the 5 Hz frequency. The instantaneous phase lag between clusters increases with distance (marked by black points), defining an oscillatory traveling wave. The dark blue outline on the left panels delimits V1. Colored circles represent the theoretical cortical locations of the simulated neuronal clusters. The WCO can be used to make each cluster correspond to a specific population Receptive Field (pRF; specific region of visual space). Brains with V1 outlines figure credit: Laura Dugué.

4 Discussion

This chapter has presented our contributions to a larger project aiming to develop a tool for model-based MEG and EEG neuroimaging. Specifically, in this thesis, we have implemented a source model with flexible parameters to mimic oscillatory propagating waves of electric activity at the surface of the cortex. We have programmed a behavioral wave inducer stimulus to elicit waves with known properties in the visual cortex. Finally, we have presented a simple computational implementation of a theoretical ensemble of neural populations giving rise to the hypothesized traveling waves of activity. Together, these tools will help characterize spatio-temporal oscillatory activity in the human cortex and uncover their role in cognition. We now discuss complementary results obtained by our team and further considerations for our tools.

4.1 Tentative inducing of waves with known and unknown parameters

Inducing semi-spontaneous traveling waves visually In a behavioral study, Sokoliuk and VanRullen (2016) aimed to induce spatio-temporal oscillatory waves in the cortex using a peripheral disk stimulus with oscillating luminance. They reasoned that an oscillatory neural signal would propagate outwards from the retinotopic location of the disk, leading to spatially propagating waves centered on the disk oscillator. The disk's temporal fluctuation would also set the temporal frequency of the cortical oscillations. In turn, the cortical waves would affect excitability across the visual cortex, thus leading to improved or impaired performance at corresponding locations in the visual field. They probed these putative cycles by presenting faint visual targets, which participants had to detect, at different locations on the screen and at different times relative to the phase of the disk oscillator. They found that participants' detection performance significantly relied on the faint target's timing and distance relative to the disk oscillator. This result was taken to support the hypothesis of spatially propagating oscillatory waves elicited by the temporally oscillating disk stimulus.

Based on this result, our team set out to further characterize these hypothesized traveling waves and their neural correlates in a new experiment. With our help, our colleague Damien Boyer designed the protocol and collected preliminary data to expand from Sokoliuk and VanRullen (2016)'s original result. He presented an identical peripheral disk stimulus with oscillating luminance. In this new version, the simple detection targets were replaced with more complex targets that could take one of two orientations. The participant's task was to report whether the target was oriented clockwise or counterclockwise. MEG was recorded while participants performed this task to correlate scalp-recorded activity with behavioral events.

This experiment was meant to constitute the first instance of inducing waves in the cortex that were not fully defined (unlike those elicited by our Visual wave inducer in Section 3.2), but whose properties were not entirely unknown either (the disk oscillator would set the origin and temporal frequency). We planned to use this data to start fitting our source model parameters and compare predicted MEG signals to the recorded ones. However, this new version failed to replicate the correspondence between task performance and the oscillating disk's phase and distance. Contrary to Sokoliuk and VanRullen (2016)'s results, these new data revealed no phase advancements with distance from the oscillating disk.

Multiple factors may contribute to these negative results. One difference between the two protocols is that the original experiment presented the oscillating disk on the upper left corner of the screen, whereas the new setup placed it at the bottom right. This location was chosen

to maximize the MEG's ability to detect oscillatory signals. However, it may be that spatial oscillatory propagation does not operate identically in the upper and lower hemispheres of the visual field, which correspond to different locations of the cortex. As we have seen, the lower half typically exhibits overall improved perceptual performance compared to the upper half. This effect may be related to oscillatory traveling effects and have thus prevented replication of Sokoliuk and VanRullen (2016)'s results. However, a third similar study from our group (Fakche & Dugué, in prep.) placed the disk oscillator at the bottom right of the screen, like in the second study, and replicated Sokoliuk and VanRullen's results, suggesting that disk placement was not the issue.

The task in Fakche and Dugué's third study consisted of a threshold detection, as in the original paradigm. They characterized the EEG-recorded oscillation waveform, revealing that this rhythm is a complex combination of the oscillator's frequency and its first harmonic (i.e., its double). We have shown in Chapter II that the frequency of neural oscillations involved in cognition may heavily depend on the specific task being performed. Thus, it may be that the temporal frequency of the evoked cortical oscillation is fluctuating too fast to influence more complex, attentional tasks, such as the one performed in our discrimination study. The discrimination experiment may have shown effects at a lower or higher frequency. An alternative explanation for the absence of phasic influence is that the discrimination task simply did not rely on cortical excitability and thus was not affected by the hypothesized spatio-temporal activity wave.

Limitations A critical problem with using visual stimuli to entrain oscillations is that all of the results may be explained by its luminance value instead of its oscillatory phase. In other words, any improvement or impairment in task performance may be due to the luminance of the oscillating disk "dimming" the targets more or less intensely. In a fourth project, our teammates have made use of a contrast-reversing checkerboard stimulus to entrain neural oscillations without relying on an absolute luminance change. However, checkerboard stimuli need to comprise a much larger portion of the visual field to elicit similar neural rhythms, thus drastically changing the visual setup. Furthermore, checkerboard stimuli introduce the added difficulty of adjusting each square to produce equal cortical representations, thus limiting the possibilities for the entraining stimuli even further. Unfortunately, with these constraints, the checkerboard oscillating stimulus could not be localized to one visual location. Thus, the point of origin of the potentially elicited traveling oscillations could not be estimated using this technique.

The ideal setup would test task performance in the absence of any visual stimulus, apart from the probing targets. It has been shown that the steady-state visual evoked potential (SSVEP) remains for a few hundred milliseconds even after the inducing stimulus has been turned off. This "ringing" or "reverberation" lasts longer if the offset coincides with a trough phase in the EEG oscillation (Breitmeyer et al., 2008). Probing performance in the absence of the visual stimulus is thus possible. We can trigger the oscillation with the disk oscillator, but instead of showing targets while the oscillator is visually present, turn the oscillator off and only then present the targets at variable short SOAs. With such a setup, we would be able to test the effect of oscillatory phase and distance, and the effects could not be explained by the differences in luminance of the visually oscillating stimulus. We may then test for the presence of traveling oscillations in behavioral and neuroimaging measures using our novel model-based methodology.

4.2 Interference of noise from spontaneous traveling oscillations

We have introduced that spatially traveling oscillations in electric activity at the surface of the cortex may serve as a "memory store" of past activity (Muller et al., 2018). Furthermore, our working hypothesis throughout this project is that sensory stimulation evokes oscillatory traveling waves and that these waves are also spontaneously generated in the cortex. Such a role for spatial oscillations implies that many of these waves occur at any given moment and location of the cortical surface. With this in mind, we might expect the cortex to be similar to a large, shallow aquarium placed directly on top of a speaker, with music (or much less structured sound) playing. Ripples and waves of different amplitudes, frequencies, and directions would travel across the 2-dimensional space. They might realistically interfere with each other and form highly complex patterns.

In this project, we have only modeled the cortex as either perfectly quiet in terms of electric activity (outside of V1), or exhibiting highly regular oscillatory propagation (in V1). However, we do not presume that our visual wave inducer would elicit cortical traveling signals in an otherwise silent cortex. If oscillatory traveling signals play a functional role in cognition, other waves may be elicited, particularly long-range waves extending to other regions which have been reported to reflect visual stimulation (Lozano-Soldevilla & VanRullen, 2019). We thus expect them to be present during our manipulations and elicit substantial noise in our recordings. This remains to be tested. However, in the case of the visual wave inducer, two factors play in our favor even if these signals are already present. The first is that, with the repetition of our inducer presentations over many trials, we will hopefully extract the oscillation of interest, while spontaneous, variable ones cancel each other out. The second favorable consideration is that we expect the waves elicited by the inducer to take on larger amplitudes than those arising from spontaneous cortical activity. Nonetheless, in future versions of the source model, we will include artificial noise with varying parameters to produce a more realistic simulation of cortical activity.

4.3 Cortical standing waves

The *standing* waves we have implemented in our designs are modeled mathematically as two traveling waves evolving in opposite directions, thus forming a highly structured spatial signal with clearly defined rings undergoing pattern reversals. These standing waves were intended as a control to test the specificity of our MEEG recordings and model predictions. There is no expected functional advantage of patterned standing waves as we have induced them using the Visual wave inducer (Section 3.2). However, irregular, patchy standing waves have been reported in the live cortex (Benucci et al., 2007). In this case, sparse patches across the surface of the primary visual cortex respond differently to stimuli orientations (horizontal or vertical). When one type of patch (e.g., tuned to horizontal stimuli) responds positively, the other (vertical) patches respond negatively and vice-versa. At the level of the entire region, this results in a standing wave (see Figure III.4.1).

Furthermore, it has been proposed that if excitatory and inhibitory connections within cortical areas show similar orientation tuning, or if signals are mainly projected in the feedforward direction, standing waves can arise (Anderson et al., 2000; Ferster & Miller, 2000). Thus, we might uncover standing waves of this type in the cortex due to the connectivity subserving orientation processing. This possibility constitutes an additional reason to make the source model as flexible and precise as possible. Our novel model-based MEEG neuroimaging tool may enable the characterization of highly localized, specific oscillatory patterns in the human cortex.

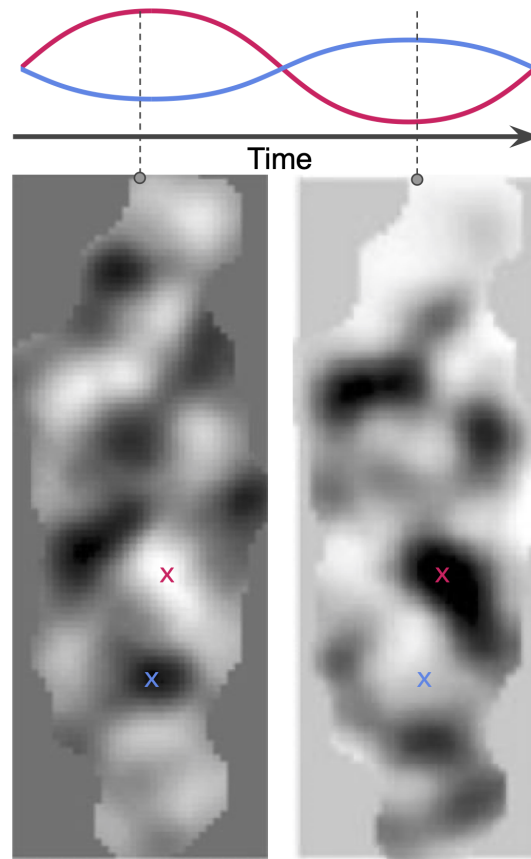


Figure III.4.1: A patchy standing wave in V1. Pink and blue traces at the top represent the time course of activity of the cortical locations marked by a pink and blue X, respectively. The two cortical images represent two single instances of the standing wave, taken at the time points indicated by dashed lines in the activity time course (top). Notice that the global pattern reverses from one half of the oscillatory cycle (left) to the next (right). The location marked by the blue X does not show as strong positive and negative activity as the location marked by the pink X: this is made evident by the difference in amplitude of their time courses (top). However, they remain in a perfect anti-phase relation. This is indicative of a standing wave, although it does not present the regular, circular pattern across the cortex like the one we have modeled (see Figure III.3.1). V1 images are adapted from Benucci et al. (2007).

4.4 Next steps for V1 characterization

We have implemented elementary first versions of the various components of our model-based neuroimaging methodology. What are the next steps in the development of this novel tool of V1 testing?

4.4.1 Amplitude and speed decays across space

The visual field is represented in a rather distorted manner in the primary visual cortex, with the center (the fovea) being magnified relative to the periphery, various asymmetries, and general non-uniformity in the mapping between external relations and its cortical representation (Connolly & Van Essen, 1984; DeValois & DeValois, 1988; Sereno et al., 1995; Strasburger et al., 2011; Tootell et al., 1988; Van Essen et al., 1984). Therefore, traveling waves in V1 may

show certain irregularities in shape, amplitude distribution, and other properties, to follow retinotopic organization. To date, these properties are not fully characterized, especially in the case of the healthy human visual cortex.

Based on reports of cortical transients rapidly fading as they travel outwards (Muller et al., 2018: see Figure III.1.1), we may expect the amplitude of oscillatory traveling waves to decrease as a function of its distance from the wave center. To account for this effect, we will include a dampening of amplitude with distance from the center in a later version of the source model.

Wave speed may also show a similar spatial decrease. Bringuier et al. (1999) found that V1 neurons' response to visual stimuli arose at a delay that showed an increase proportional to the stimulus' distance from the neuron's receptive field. In other words, the further a neuron is from the retinotopic location of the stimulus, the more slowly the signal reaches it. This correspondence of delay to distance is compatible with the speed of lateral connections in the cortex (Girard et al., 2001). These results from hyper-localized intracellular recordings lead us to expect the speed of cortical waves to decrease away from the origin. Future versions of the source model will include this effect as well.

Finally, the direction of propagation of these recorded spatio-temporal oscillatory signals seems to depend on the task: in some cases, they travel from posterior to frontal regions (Fellinger et al., 2012; Klimesch et al., 2007a), but in others, this direction is reversed (Patten et al., 2012). A long-term aim of the collaborative project is thus to test multiple directions of propagation in healthy, neurotypical humans. Similarly, a tool to capture the spatial displacement (phase) of cortical waves will be needed.

4.4.2 Considerations for the WCO model

Such a decrease in traveling speed across space may support the weakly coupled oscillator (WCO) model, which we have begun to implement (Section 3.3). Indeed, in the WCO model, oscillators exhibit decreasing intrinsic frequency across space. We may link this to the above findings: away from the retinotopic location of the visual stimulus, the lateral connections along the surface of the cortex lose strength and thus become slower. This speed gradient is conducive to creating a gradient of frequencies, as is modeled in the WCOs. The WCO model can thus be a close reflection of V1 activity.

If the above considerations hold, we may further flesh out the WCO model to approximate the expanding traveling waves modeled in the MEEG sources and visual wave inducer. Indeed, instead of the individual oscillators being arranged in one line, they may be placed all around the origin in a two-dimensional spatial organization. In this new setup, the oscillators closest to the origin would exhibit the fastest intrinsic frequency, in line with Bringuier et al. (1999)'s intracellular findings. Such a simulation would constitute an exciting test of weakly coupled oscillators' ability to generate waves similar to the ones implemented in the source model.

4.4.3 Anisotropy

Because the visual field is far from being represented uniformly in the cortex and asymmetries exist between visual processing at different locations (e.g., top and bottom hemifields, Portin et al., 1999; Van Essen et al., 1984), waves with non-uniform spatial properties may maximally serve visual processing. Such non-uniformity across the different directions of effect is termed "anisotropy." We wish to test for anisotropic waves using our novel tool, which will require implementing anisotropy in our models. For example, the amplitude of the oscillations may differ in opposite directions, and its decay may proceed faster or slower depending on relative retinotopic location. Aside from amplitude, anisotropy may affect any property. Thus, a subsequent step for the source model will allow for the separation of values according to direction for each parameter (e.g., speed and frequency).

4.5 New perspectives

Now that the V1 model is underway, we consider how our novel tool can be further developed to include more functions and regions. Our hope for this methodology is that it will aid many investigators of the relation between mind and brain to characterize waves in their regions and tasks of interest.

4.5.1 Expanding our cognitive reach: attentional manipulations

Our Visual wave inducer provokes exogenous, sensory-driven V1 waves, which likely exhibit much stronger amplitude than the spontaneous traveling waves reported in the literature. Nonetheless, spontaneous waves are likely present during wave inducer viewing. We have seen that even low-level visual areas such as V1 are modulated by attention (see General Introduction Section 2.2.2). We speculate that traveling waves partially mediate this modulation. Thus, spontaneous, attentional traveling waves may be propagating during presentation of the Visual wave inducer due to the attentional task on the central fixation point. Different versions of the task will be necessary to make the difference between induced sensory waves and spontaneous, functional waves. Spontaneous traveling waves may arise from perception, attention, or other functions: these links also remain to be tested.

Many of the experiments performed in the studies reporting oscillatory dynamics do not explicitly manipulate attention, nor do they control for its effects. In one example among many, the visual stimulus in Dugué et al. (2011)'s study always occurs at the same location in the visual field, so the participant's attention is almost certainly maintained at that location, although this is not explicitly tested. While developing our methodological tool, we were concerned primarily with visual perception, but we tested it with concurrent attentional focus. In future work, it will be interesting to investigate the effect of attention. Specific manipulations may allow us to test whether attention alone correlates with spatially propagating waves. A key manipulation will be to orient participants' attention non-visually, e.g., using an endogenous cue, and apply our novel methodology to measure any related traveling oscillations. We may also simultaneously present an oscillating perceptual stimulus and an attentional task at a different location to check for interference between them. Future manipulations of this kind, supplemented with our novel tools for model-based neuroimaging, will allow us to test the specific contributions of perception and attention to spatio-temporal dynamics in the human cortex.

4.5.2 Expanding the cortical reach

Different brain areas exhibit high similarities in terms of cortical processing (Creutzfeldt, 1977). Thus, characterizing V1 may give us valuable tools for describing other, less well-studied areas later on. For example, a portion of inferotemporal (IT) neurons show retinotopy (spatial tuning), but this area is primarily feature-tuned (Schwartz et al., 1983). This and other specificities will need to be taken into account when generalizing to other visual areas outside of V1. Furthermore, the attentional enhancement of retinotopic fMRI BOLD responses gets stronger along the visual hierarchy, with a more robust modulation in extrastriate than striate areas (Liu et al., 2005). Testing these peri-V1 areas may shed light on the involvement of traveling oscillations in visual attention.

By determining spatial oscillatory properties in the occipital lobe, we will also hold at least the first keys to characterize similar mechanisms in higher or other-modality areas. It will be of high interest to perform similar tests in non-visual cortical regions. Down the line, we wish to expand our view from within-area testing and consider inter-regional communication using our novel tools. More far-reaching oscillatory traveling waves, e.g., traveling from the occipital cortex out to parietal and frontal regions, may facilitate communication between these

regions during complex tasks. Our flexible modeling tool will allow adaptation to simulate these long-range signals and thus aid their uncovering too.

4.6 Spatial dynamics: conclusion

We have now presented multiple hypotheses of the spatial organization of oscillatory cortical activity. The *stationary* spatial hypothesis posits that oscillations arise at disparate locations on the cortex, depending on the task and the regions involved in processing, and that these oscillations interact via temporal dynamics only. On the other hand, the *traveling* spatial hypothesis (including both propagating transients and oscillations) models a physical displacement of the signals along the cortex. It may seem like these theories mutually exclude each other, but this is not the case. Stationary oscillatory coupling, traveling transients, and oscillatory traveling waves are not incompatible. The models of stationary spatial coupling presented in the General Introduction (Section 3.4) do not assume that oscillatory signals travel, but their mechanisms do not exclude this possibility either. Furthermore, single-front transients and multi-cycle oscillatory waves may very well both exist in the brain, perhaps subtending subtly different mechanisms. These two types of traveling signals could both contribute to the spatial dynamics of cortical activity. We hope that our novel tools and models will shed light on the characteristics and function of oscillatory traveling waves and bring the field closer to a complete understanding of neural spatio-temporal organization.

IV

GENERAL DISCUSSION

Low-frequency rhythms are crucially involved in cognition. This thesis showed that subtle task differences affect the precise frequency of the neural oscillations reflecting attentional performance. These task differences may explain the wide range of disparate frequencies that correlate with perceptual and attentional performance across the literature. We reviewed how low-frequency rhythms may be implemented by signals traveling at the surface of the cortex, most likely implemented in horizontal connections between cortical neurons. We began the development of a computational model to measure and understand these traveling signals. We presented our novel methods for the implementation of model-based magneto- and electro-encephalography (MEEG).

Other elements remain open to discussion: we will now address outstanding questions and issues in the field of neural oscillations and their relation to cognition.

1 Oscillations in cognition

1.1 Early pre-stimulus phase effects

Our study of the temporal dynamics of neural signals during visual search (reported in Chapter II) showed that pre-stimulus alpha oscillations' phase predicted participant performance. Our report is far from the first to report such an effect of spontaneous alpha phase on behavior (e.g., Busch & VanRullen, 2010; Hanslmayr et al., 2013; Mathewson et al., 2009; Myers et al., 2014; Samaha et al., 2017). In our and past studies, significant phase opposition sum (POS) is typically reported early, long before the experimental event of interest. Sometimes, it may be found as far back as 800 ms before stimulus onset (Dugué et al., 2011; Romei et al., 2008).

This observation yields an intuitive and relevant question. If POS is meant to reflect the behavioral influence of instantaneous oscillatory phase at the moment of stimulus appearance, should it not peak precisely at that moment? Contrary to this intuition, in many examples, POS is null from stimulus onset forward (Busch et al., 2009). Considering the time taken for the information to reach the cortex (~100 ms), we may even expect the POS to peak sometime *after* stimulus onset. With this in mind, why is the effect found at such early times? Should we take it to mean that the system has to fall into a favorable phase *before* the stimulus appeared, perhaps to prepare for the upcoming stimulation, and that phase no longer matters after this preemptive window?

In practice, multiple factors influence our calculations of pre-stimulus phase effects. Morlet wavelets are typically convolved with the signal in sliding windows to extract frequency, amplitude, and phase information. These wavelets necessarily extend in time, especially in the low-frequency bands, where cycles are longer. This temporal extent means that the wavelet may carry information forward or backward in time, thus causing contamination from previous or subsequent periods (McLelland et al., 2016). This contamination is especially prominent in the case of the post-stimulus evoked response potentials (ERPs), which cause major disruptions in temporal dynamics (VanRullen, 2016b). For these reasons, the pre-stimulus POS should not be taken to reflect the full dynamics of phase influence. It should instead be seen as the earliest, uncontaminated window accessible to the decomposition. Considering these factors, early phase opposition measures may still be interpreted as reflecting an influence of instantaneous phase at stimulus onset.

1.2 What is the functional role of alpha inhibition?

As we have seen in General Introduction Section 3.4 on the hypothesis of gating-by-inhibition, the alpha rhythm may serve to deliver pulsed inhibition waves to silence cortical regions not currently in use (Jensen & Mazaheri, 2010). What might be the use for the brain to implement such organized inhibition? More specifically, if one function of alpha oscillations is to reduce processing in given areas purposely, why do we observe it so clearly in certain participants' visual cortex when they close their eyes? With eyes closed, no visual stimuli can distract us, so it seems like we would not require such inhibition. However, we might make sense of this when we consider that mental imagery recruits sensory areas (Albers et al., 2013; Knauff et al., 2000). Perhaps, when the individual's eyes are closed, the alpha rhythm suppresses occipital activity while mentally picturing stimuli. Alpha inhibition could thus ensure that the individual knows that what they mentally picture is not happening in the external world. If this were the case, we should observe stronger alpha amplitude while performing vivid mental imagery than when the mental canvas is blank. Experimental evidence validates this prediction (Bartsch et al., 2015). This finding further supports the inhibitory nature of alpha oscillations and provides evidence of its functional role as a guardian of reality.

1.3 Alpha power as a marker of excitability, not perceptual performance

Thus, alpha amplitude is classically seen as a marker of inhibition, both from the neural (Haegens et al., 2011; Lőrincz et al., 2009) and behavioral (e.g., Händel et al., 2011) point of view. In many studies, the focus has been on the correlation between alpha amplitude and perceptual performance. However, Lange et al. (2013) argue that the link is not so direct. Their ingenious manipulation of clearly visible (but temporally ambiguous) flashes demonstrates that reduced pre-stimulus alpha power leads to a greater excitability, which may either aid or impair perception. A low amplitude in pre-stimulus alpha raises the observer's hit rate *and* false alarm rate. This effect can thus lead to better or worse overall task performance, depending on whether it is beneficial or detrimental to perceive stimuli more readily (even if they are illusory). In the next sections, we will review studies probing cortical excitability and see how these contribute to this hypothesis.

1.4 Are oscillations involved in cognition, or simply an epiphenomenon?

Many authors reject any consideration of cerebral oscillations as functional mechanisms, dismissing them as an "epiphenomenon" with no intrinsic value. In this thesis, we have mainly discussed correlations between neural oscillations and their associated cognitive phenomena. By these accounts, oscillations and corresponding behavioral effects may not be directly related but emerge from a common cause. However, strong evidence from other experiments supports the causal role of neural oscillations in cognition.

As we have seen, the relative amplitudes of low- and high-frequency neural rhythms reflect cognitive functioning (e.g., Llinas et al., 2007). Recent studies making use of non-invasive brain stimulation (NIBS) take oscillatory experimentation one step further by testing the causal links between neural rhythms and cognition (Peylo et al., 2021; Silvanto & Muggleton, 2008). Not only do oscillations correlate closely with cognitive functions, as we have seen, but they causally impact cognition when manipulated with stimulation, as made evident using transcranial alternating and direct current stimulation (tACS and tDCS, respectively; Antal et al., 2003; Kanai et al., 2010; Paus et al., 2001; Thut, 2014; Zhang et al., 2019), transcranial magnetic

stimulation (TMS; Romei et al., 2010), and even sensory entrainment (Thut et al., 2012). Doubts were raised concerning whether rhythmic TMS truly entrained neural oscillations, thus putting into question their causal role in cognition as tested by NIBS techniques. Perhaps TMS was causing behavioral effects through other means. However, a recent review by Romei et al. (2016) gathers evidence that TMS entrains neural rhythms, further supporting their causal, functional influence. Finally, intracortical entrainment using optogenetic manipulations demonstrated that cortical oscillations cause perceptual modulations in mice (Cardin et al., 2009; Knoblich et al., 2010; Siegle et al., 2014). With these interventional studies and their positive results in mind, it is difficult to reject the causal influence of oscillatory properties on cognition.

2 Effects of different cognitive functions

We have mentioned in Chapter II the limitations of visual search in testing the separate effects of perception, attention, and memory. Indeed, these three functions have highly overlapping outcomes in behavior, making them extremely difficult to disentangle from one another. Identifying their neural correlates, which additionally requires recording from the live, awake brain, thus presents a tremendous challenge (Clark et al., 2015). It remains essential to understand their separate contributions to cognition and differentiate them in cognitive neuroscience studies.

2.1 Distinctive views on primate brain structure

Region-to-function mapping It has been proposed that the view of a direct, one-to-one mapping between cortical regions and cognitive functions is an oversimplification (Clark et al., 2015). There may not exist a clear-cut differentiation between cognitive functions at the level of the brain, although researchers typically try to find specialized neurons and areas (Churchland et al., 2012; Mante et al., 2013; Raposo et al., 2014; Rigotti et al., 2013). We have seen that the cortical attentional network seems more extensive in humans than nonhuman primates (General Introduction, Section 2.2.4). Human attention may thus interact more extensively with memory functions, which are thought to recruit distributed areas of the frontal and parietal cortices (Blumenfeld & Ranganath, 2007; Lara & Wallis, 2015; Vilberg & Rugg, 2008). The anterior cingulate cortex (ACC), a region of the human attentional network, also shows elevated activity for incongruent trials in the Stroop task, which tests cognitive inhibition and response suppression (Pardo et al., 1990). This bipartite role of the ACC suggests that this region is involved in a broader network of processing modulation and conflict resolution. Tasks designed specifically to test the difference in neuronal activation between attentional, memory-related, and other executive functions (Fedorenko et al., 2013) suggest that frontal and parietal regions may be involved in versatile cognitive functioning. These regions would potentially enable us to solve new, unusual problems. At the microscopic scale, individual neurons were found to reflect multiple functions (Lebedev et al., 2004). These observations attest to the flexibility of the human cognitive system and indicate a divided role for the regions labeled as attentional. We may instead consider a broader network of *adaptability*. Nonetheless, the current overarching view that areas of the cortex have specialized subfunctions for cognition has yielded vital predictions. It has effectively guided experimentation on neural processes and remains the dominant philosophy in our understanding of the cerebral cortex (Markov et al., 2014).

The cortical-centric view The evidence reported in this thesis heavily relies on scalp-recorded activity and cortical recordings, so our focus has targeted the neocortex. However, subcortical areas also constitute essential components of these cognitive networks. We have seen that the lateral geniculate and thalamic reticular nuclei (LGN and TRN) of the thalamus are modulated by attention much like low-level visual cortical regions (McAlonan et al., 2000; Vanduffel et al., 2000). Furthermore, the pulvinar nucleus of the thalamus is thought to exert attentional control similar to high-level attentional areas (Kastner & Pinsk, 2004). The superior colliculus (SC), a non-thalamic subcortical region, has shown similar high-level attentional involvement. Apart from receiving visual input from the retina for relaying to various structures and orienting saccades (Robinson, 1972), certain layers of the SC have been related to covert attentional processes, making it an integral part of the attentional network (Lovejoy & Krauzlis, 2010). It is preferentially activated by salient, "pop-out" stimuli (McPeck & Keller, 2002), but also shows evidence of top-down modulation, much like the visual cortical areas (Shen & Paré, 2007). Perhaps most convincingly, inactivation of the SC causes the inability to ignore distractors, even in the absence of eye movements (Lovejoy & Krauzlis, 2010). A large body of evidence, from lesion studies (Danziger et al., 1997; Posner et al., 1985; Rafal et al., 1988; Sapir et al., 1999) to physiological reports (Dorris & Munoz, 1995; Dorris et al., 2002; Rafal et al., 1989), has shown the necessary involvement of the SC in attentional inhibition of return, i.e., the tendency to ignore a location immediately after it has been attended, and favor unexplored loci (Klein, 2000). These results attest to the indispensable nature of the SC in normal attentive functioning. Throughout this thesis, our considerations of the neural bases almost exclusively centered on neocortical areas: perhaps subcortical structures are more involved in attention than this view allows. Of course, recording from these areas is difficult, especially in live, healthy humans. The imaging tools with sufficiently reliable spatial resolution to expose subcortical nuclei, such as fMRI, do not possess the temporal resolution to measure sub-second oscillatory dynamics. More advanced neuroimaging technology will be needed before we can truly assess the contributions of subcortical regions in spatio-temporal attentional coordination.

2.2 The difference between attention and memory

The typical method used to isolate a function is to compare conditions to subtract any potential influence except the studied one. We have introduced that, thanks to valid and invalid cueing, we can extract the effects of attention independently from memory because valid and invalid trials recruit the same memory components. However, many studies do not systematically control for this memory confound, making it unclear whether the reported neural correlates reflect attention, memory, or both.

We have mentioned Saalman et al. (2007)'s study in the General Introduction. In this typical example, the authors refer to their effects as resulting from attentional differences, but it is not clear from their behavioral manipulation whether they are probing attention, memory, or both. The monkeys performing the task must "attend" to a given location or feature depending on the trial. However, to trigger "attention," the experimenters present a first stimulus, followed by a second one after a delay. The monkey is trained to report whether the second stimulus matched the first, both in terms of physical attributes and spatial location. In other words, the monkey has to *remember* the appearance and location of the first stimulus until the second one appears. It follows that all of the effects reported in this study may be attributed to memory processes. Because the authors refer to them as attentional, the literature has relied on this study to argue for a link between the reported neural recordings and attention, although the evidence cannot support this claim. Fortunately, in this case, other studies explicitly targeting the different contributions of attention and memory have backed these results (e.g., Lebedev et al., 2004). One experiment further revealed that cortical areas and even individual neurons show involvement in both memory and attentional processes, suggesting that these functions

are intertwined at the neural level as well (Ikkai & Curtis, 2011).

This example illustrates the importance of combining high-quality behavioral paradigms with neurophysiological recordings. As we have discussed in Chapter II, visual search in its classic form is not adapted to differentiate between the effects of perception, attention, and memory (Bahle et al., 2020). We have maintained trial durations under 600 ms in our visual search experiments, making it unlikely to involve working memory, although it does not rule out immediate memory effects. However, a recent study has adapted the classic visual search paradigm (Kong & Fougne, 2021) and used it to demonstrate that attentional selection in perception does not exhibit the same behavioral effects as attention to memory. Thus, despite its shortcomings, visual search remains a powerful tool to study these cognitive functions. It has been instrumental in guiding our understanding of the complex process of searching for an item among irrelevant elements, a skill we regularly employ in our daily lives. This paradigm has considerably advanced the collective knowledge of complex cognitive functioning. Our study of temporal dynamics in scalp-recorded activity during visual search has provided a more detailed characterization of the neural oscillations involved in such tasks.

2.3 Perception and the hypothesis of "unsolicited attention"

We are under the impression that visual information is flowing into our consciousness continuously, without any breaks, as if our perceptual system received constant input. Throughout this thesis, we have shown evidence refuting this subjective experience, suggesting that perception is not continuous. Indeed, this impression is strong, but it must be wrong: if we perceived our visual environment continuously, we would see the individual static images that make up most videos (24 Hz), but we do not. This fact suggests that we process the visual field at a lower rate and fill information in between samples, creating the illusion of a continuous flow.

On the other hand, we see individual static pictures if random images, instead of similar ones, are presented at the same rate. These seemingly opposing effects can be resolved if we consider that our perceptual sampling operates at different frequencies depending on stimulus properties. We might integrate motion information at low rates, thus readily perceiving motion between similar images in a typical movie. In contrast, we would integrate intense luminosity changes at a higher rate, making it possible, for example, to perceive the flashes of strobe lights at very high rates. Indeed, as VanRullen (2016b) reviewed, rhythms of multiple frequencies seem to be involved in perceptual processes. As we have argued in Chapter II, these frequency differences may result from the discrepancy in tasks performed and stimuli presented. For example, perceptual performance is reported to fluctuate at temporal rates in the theta and alpha ranges (4-12 Hz; Dehaene, 1993) and to be associated with corresponding scalp-recorded rhythms (Ergenoglu et al., 2004; VanRullen & Macdonald, 2012). A recent report also shows the influence of other bodily factors, such as respiration, on the correspondence between alpha rhythms and perceptual performance (Kluger et al., 2021). These much slower rhythms have thus been attributed to perception, but this may confuse perception's meaning, particularly its difference with attention.

As we have seen, attention also fluctuates periodically and correlates with brain oscillations of low frequency. In our experimental report (Chapter II), we have newly shown that resolving visual searches with increasing complexity correlates with neural rhythms in the theta and alpha ranges. There can (and must) be forms of "unsolicited attention," i.e., attentional processes that are ongoing regardless of the experimental manipulation, much the same way perception is ongoing even when it is not the topic of study. These slower rhythms deemed "perceptual" can thus arguably be re-categorized as "attentional."

Disentangling perceptual from attentional rhythms is challenging, but experiments with this aim are needed to better understand their particular contributions. Cueing paradigms have been used to begin answering these questions (Senoussi et al., 2019), but adapting visual

search paradigms as we have suggested may also provide informative evidence. It will be of high interest to test the differentiated effects of attention and perception on both the temporal and spatial properties of neural oscillations, as discussed in Chapter III. We hope that our novel tool for model-based neuroimaging will help to uncover the subtle links between cognitive functions and spatio-temporal neural dynamics.

3 Conclusion

We have shown that scalp-recorded oscillations' precise temporal and spatial properties are both crucial markers of neural activity and, further down the line, of cognition itself. We have explored the spatio-temporal dynamics of neural oscillations, first through the behavioral manipulation of visual search tasks with simultaneous EEG recording and subsequently via computational modeling of the visual cortex. Our contributions do not resolve the question of the role of oscillations in cognition and behavior, but they support a close link between them. Many more tests are required to flesh out the remaining unanswered questions, added to those newly arisen from our work. The young field of research on the role of neural oscillations in human behavior remains a largely unsolved puzzle, but we hope to have placed a few of the pieces where they belong.

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