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Thèse de Doctorat, Université Paris Descartes

Hemispheric differences in preparatory attention: a divided visual field study

Différences hémisphériques de l'attention préparatoire: une étude en champ visuel divisé

Laura Gabriela Fernandez

Sous la direction du Pr. Eric Siéroff

Université Paris Descartes

Ecole Doctorale 261

« Cognition, Comportement, Conduites Humaines »

EA 4468 Equipe Neuropsychologie du vieillissement

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Thèse de doctorat de Psychologie Cognitive

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Résumé

Un aspect fondamental du contrôle attentionnel réside dans la capacité du sujet à anticiper l'apparition d'un stimulus afin de rendre son traitement plus rapide et plus efficace. L'attention préparatoire (AP) est la capacité de moduler (rehausser) l'intensité de l'attention dirigée vers un stimulus sélectionné avant son apparition, en empêchant que le sujet soit distrait par une information non pertinente. Certaines études soutiennent que l'AP est latéralisée dans l'hémisphère droit (HD) alors que d'autres suggèrent que les deux hémisphères, l'hémisphère gauche (HG) et l'HD, sont impliqués dans la modulation de l'AP. L'objectif de cette thèse est d'analyser le rôle joué par chaque hémisphère cérébral dans la modulation de l'AP dirigée vers une localisation de l'espace. Nous avons développé une version latéralisée du test APT (pour *Attentional Preparatory Test*, proposé par LaBerge, Auclair & Siéroff, 2000), le LAPT (*Lateralized Attentional Preparatory Test*). L'APT permet de mesurer la capacité des sujets à moduler leur AP vers la localisation d'une cible lorsque la probabilité d'un distracteur varie selon plusieurs blocs d'essais. Dans l'APT, le temps de réponse augmentait lorsque la probabilité d'apparition d'un distracteur dans la phase préparatoire antérieure à la présentation de la cible augmentait, ce qui montre que l'AP est modulée par des évènements antérieurs au traitement de la cible. Nous avons créé le LAPT en utilisant la méthode de présentation en champ visuel divisé dans laquelle les stimuli peuvent apparaître dans le champ visuel gauche (CVG) ou dans le champ visuel droit (CVD). Les différences de performances entre champs visuels nous donnent des indications sur les stratégies de traitement des deux hémisphères (CVD/HG vs CVG/HD). Dans une série d'études, nous avons montré que la modulation de l'AP en fonction de la probabilité attendue d'un événement diffère dans chaque champ visuel/hémisphère en fonction de la configuration de la tâche. Dans le CVD/HG, l'AP est modulée par la probabilité des événements distracteurs, surtout quand cette probabilité est explicite. De plus, l'HG semble tenir un rôle crucial dans la modulation de l'AP quand la cible et le distracteur sont difficiles à discriminer. Dans le CVG/HD, l'AP est modulée par la probabilité temporelle des événements et dépendrait du délai le plus probable dans lequel la cible est attendue, mais seulement lorsque la discrimination entre la cible et le distracteur est plus facile. Enfin, nos résultats suggèrent que les différences entre le CVD/LH et le CVG/RH lors de cette modulation attentionnelle se mettent en place à un niveau perceptif du traitement de l'information car ils sont indépendants de la main utilisée pour répondre et donc des processus requis au niveau de la programmation motrice. L'ensemble de ces résultats suggère que chaque hémisphère utilise une stratégie différente pour moduler l'AP lorsqu'elle est dirigée vers une localisation de l'espace.

Mots clés : attention préparatoire ; spécialisation hémisphérique ; probabilité ; stratégies ; méthode du champ visuel divisé

Abstract

A crucial aspect of attentional control is the capacity of anticipating a stimulus appearance in order to improve the speed and effectiveness of its subsequent processing. Preparatory attention (PA) is the ability to modulate (enhance) the intensity of attention directed to a selected stimulus prior to its occurrence, preventing subjects from being distracted by interfering stimuli. Some studies propose that PA is lateralized to the right hemisphere (RH) while others suggest that both the left hemisphere (LH) and the RH participate in the modulation of PA. The aim of the present thesis was to examine the role of each brain hemisphere in the modulation of PA directed to a spatial location. We developed a lateralized version of the *Attentional Preparatory Test*, (APT, proposed par LaBerge, Auclair & Siéroff, 2000), named the Lateralized APT or LAPT. The APT measures the ability of subjects to modulate PA directed to a target location when the probability of a distractor occurrence varies across several blocks of trials. In the APT, the response times increased as the probability of a distractor appearing in the preparatory phase preceding the target presentation increased, showing that PA is modulated by the events occurring prior to the target appearance. We developed the LAPT using the divided visual field paradigm in which stimuli can occur in the left (LVF) or the right (RVF) visual fields. The visual field differences in subjects' performance are assumed to reflect differences in the processing strategies of both hemispheres (RVF/LH *vs* LVF/RH). In a series of studies we showed that the modulation of PA by the expected probability of events was different in each visual field/hemisphere, depending on task configuration. In the RVF/LH, PA is modulated by the expected probability of distractor events, especially when this probability is explicit. In addition, the LH seems to play a crucial role in modulating PA when the target and the distractor are hard to discriminate. In the LVF/RH, PA is modulated by the temporal probability of events and may depend on the most probable delay in which the target is expected, but only when the discrimination between the target and the distractor is easy. Most importantly, our findings suggest that the differences between RVF/LH and LVF/RH in the modulation of PA take place at the perceptual level of processing because they are independent of the hand use in executing the response, thus also independent of the processes taking place at the motor programming level. Taken together our results, they suggest that each hemisphere uses a different strategy to modulate PA when directed to a spatial location.

Key words: preparatory attention; hemispheric specialization; probability; strategies; divided visual field method

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INTRODUCTION

The ability to anticipate the occurrence of a future event is a crucial aspect of attentional control. The intensity of attentional activity directed to an expected event can be modulated by different characteristics of the environment. When we are waiting at the bus station and the bus is about to come, our attention might exclusively be directed to the anticipation of the bus features. We can hold a mental representation of the bus size, number and color to make it stop as soon as we see an image that matches the one we have in mind. If taking this bus is crucial for arriving on time to an important meeting, the amount of attention directed to process the expected information is increased. In other words, the motivational aspect of the expected event can modulate the intensity of attention directed to it before its occurrence. When we are reading a crime novel, and we are about to arrive to the moment in which the identity of the person who committed the crime is unveiled, our attention is directed to process the information arising from the written lines. Our concentration on the content of the novel might prevent us from being distracted by other events in the surrounding environment, such as someone entering the room, or a bird landing on our window.

These daily situations are examples of the behavioral benefits of the ability to allocate attention to an event prior to its occurrence, an ability known as preparatory attention (PA). Increasing the amount of PA directed to an event increases the speed of that event processing and prevents us of being distracted by interfering events. The amount of attentional activity directed to an expected event is modulated by our momentary goals and motivations and by the information accumulated from past events. If I spill several drops of coffee on a white tablecloth when serving a cup, this event may modulate the amount of PA directed to the act of serving the next cup to avoid repeating the consequences of the last behavior. The frequency of this unwanted behavior influences the expectation of its occurrence, and thus modulates the intensity of PA allocated to the act of serving in the future. This means that the intensity of attention directed at an event before its occurrence is modulated by the relative frequency with which that event occurred in the past.

Research in cognition has shown that different brain regions are involved when attentional activity is directed to an expected stimulus before its appearance. PA recruits cortical and subcortical areas in order to pre-process the expected stimulus, forming a

particular neural network (LaBerge, 1995, 1997). This network includes frontal areas exerting attentional control connected to posterior areas of sensory processing. The modulatory function of the frontal cortex towards posterior regions in preparation of a stimulus has been widely studied. However, it is not yet clear whether there is one mode of information processing in PA or different modes depending on task configuration. One level at which the modes of processing can differ is the hemispheric level. Several studies proposed that the brain hemispheres are specialized in different modes of processing specific information, suggesting the lateralization of different cognitive and behavioral functions. Specifically, some investigations have proposed that PA is lateralized to one hemisphere, particularly the right hemisphere (RH), while others indicated that both the RH and the left hemisphere (LH) participate to the modulation of PA in a different manner. The question of whether PA is lateralized to the RH or differently modulated by each hemisphere remains unanswered. The aim of the present thesis is to address this question by investigating the role of each brain hemisphere in the modulation of the intensity of PA directed to a spatial location.

LaBerge, Auclair and Siéroff (2000) proposed a simple paradigm to measure the cognitive capacity of modulating the amount of PA directed to a spatial location. By varying the probability of a stimulus appearance in a certain location across different block of trials, they demonstrated that the relative frequency with which a stimulus appeared in that location modulated the intensity of PA directed to that region in space. In the present thesis, different lateralized versions of this paradigm were developed to test the ability of hemispheres to allocate PA to a spatial location. We presented stimuli using the divided visual field method, in which stimuli can occur in the left visual field (LVF) or the right visual field (RVF). Since the visual pathways are crossed, a stimulus presented in the LVF is first processed by the RH and a stimulus presented in the RVF is first processed by the LH. As a consequence, visual field differences in subjects' performance are assumed to reflect differences in hemispheric functioning. The divided visual field method is considered an efficient and useful tool to investigate hemispheric differences in PA on neurological normal individuals.

This thesis is organized in two main parts: in the first part, a review of the literature about the subject of investigation is introduced, and in the second part, a group of new experiments is presented. The first part is sub-divided into three chapters. Chapter 1 introduces the concept of PA and presents different factors that play an important role in modulating the intensity of PA directed to an event. Chapter 2 presents the brain regions shown to be recruited in PA and a theoretical model to frame the study of PA. In this chapter

an experimental paradigm to measure the preparatory attentional activity directed to a spatial location is also presented. Finally, Chapter 3 deals with behavioral and neurological hemispheric asymmetry in visual attentional processes. A significant part of this chapter is devoted to the description of two main hypotheses related to hemispheric differences in the modulation of PA.

In the second part, seven behavioral experiments are presented, organized in five Chapters. Chapter 4 (Experiments 1 and 2) focuses on the hemispheric modulation of PA across the visual field in relation to the probability of events occurrence in a spatial location. The performance of neurologically normal subjects in a new lateralized version of the test developed by LaBerge et al. (2000) is presented. Chapter 5 (Experiment 3) addresses the question of the influence of events' temporal probability in the modulation of PA by each hemisphere. Chapter 6 (Experiments 4 and 5) considers the hemispheric modulation of PA towards a spatial location when the probability of events is learned from the sequence of trials. This chapter also examines the influence of the task performed by subjects on the hemispheric modulation of PA. Chapter 7 (Experiment 6) addresses the question of hemispheric capacity of reinforcing the intensities of PA to a specific spatial location by means of an instruction. Finally, Chapter 8 (Experiment 7) deals with the topic of the modulation of PA when the discrimination between stimuli has different levels of difficulty. In this Chapter the influence of the spatial proximity between stimuli in the hemispheric modulation of PA is tested.

To summarize, the central purpose of this thesis is to examine the role of each hemisphere in the voluntary allocation of attention at an early stage of information processing. We will show visual field differences in the modulation of PA directed to a spatial location. These differences are related to the differential processing of stimuli probability in each visual field, depending on task configuration. The visual field differences are interpreted within the framework of hemispheric differences in the strategic modulation of PA at the perceptual level of processing.

PART 1: Literature review

CHAPTER 1: Preparatory attention

1.1. Introduction to the concept of PA

In everyday life we are confronted with an incredibly amount of visual information. To deal with this information, our perceptual system has to select a signal (relevant information) and separate it from noise (irrelevant information). This selective process implies that some information is momentarily excluded from processing. The system's prioritization of some aspects of information (e.g. a visual location) may occur by operations that either enhance the information arising from the target object, or by operations that suppress the information arising from distractors in the surrounding environment, or by operations that do both.

There has been a long debate about whether these operations occur early or late in the flow of information (see Fig. 1). The early selection approach (Broadbent, 1958) states that attentional selection occurs prior to the identification process (sensory stage of processing), and the operations of identification apply only to the target object and not to the other objects in the scene. The late selection approach (Deutsch & Deutsch, 1963) assumes that all objects are identified in a visual scene and that the selection process occurs only later in order to provide an overt response (decision stage of processing). Experimental data demonstrates that selection can occur early or late depending on the task to be performed (Navon, 1989). If the selection is based on a physical characteristic of the object (e.g. color, spatial location, etc.) there will be an early selection of the information, in order to decrease the irrelevant information. In contrast, selection will occur later in the information processing when the task involves the selection of high level object information (such as its identity), and when the object is familiar. In the present study, we were interested in the early allocation of attention to visuo-spatial locations.

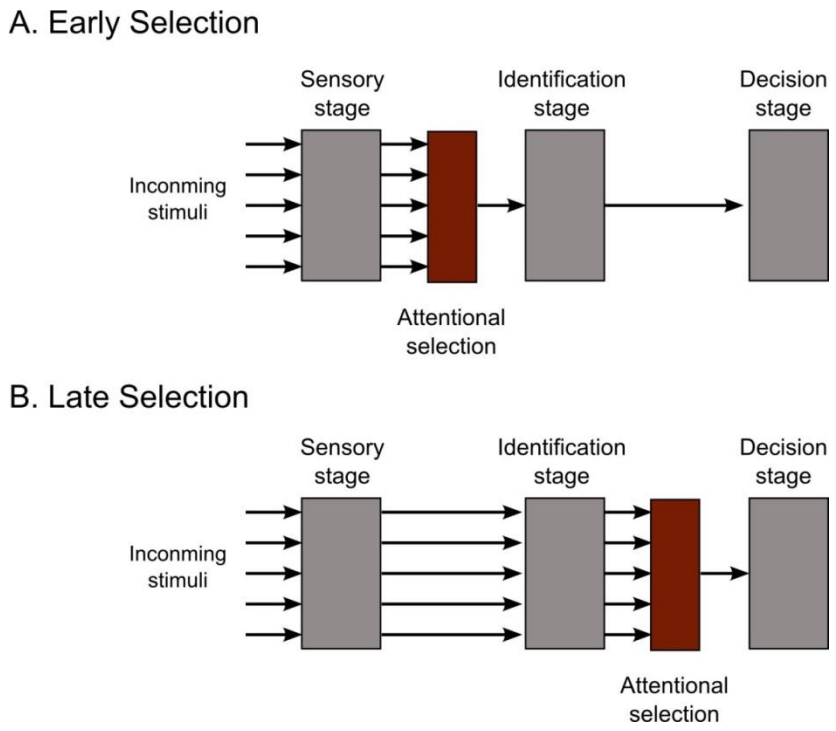

Figure 1. Schematic diagrams depicting two different accounts of attentional selection (red rectangles) in the flow of information in (A) the early selection account (Broadbent, 1958), and (B) the late selection account (Deutsch & Deutsch, 1963).

Different theoretical models have been proposed to describe how attention operates in the visual field. Visual attention has been linked to a spotlight that can be oriented by subjects' will (Posner, 1980). The orientation of the attentional spotlight to a spatial location facilitates the processing of information in that region of space. Therefore, the location of the spotlight is a crucial component of facilitation processing, as it predicts a cost in shifting attention elsewhere. Another proposal is that attention acts as a zoom lens and the size of visual attention focus can be manipulated. According to the zoom lens model, the resolution of visual selection can vary with the size of the attentional focus (Eriksen & St. James, 1986). The larger the size of the attentional field, the smaller the resolution in attentional operations. However, these models of visual attention do not explicitly separate the attention generated prior to a stimulus display from attention generated at the time of the stimulus display appearance. In an attempt to account for these two processes, LaBerge (1995, 1997) proposed a different model to frame attentional operations.

LaBerge (1995, 1997) distinguishes three aspects of attention: selection, preparation, and maintenance. Selection, or brief attention, is a rapid process (a fraction of a second)

required, for example, to discriminate between targets and distractors when they are presented simultaneously. Preparation is a slower process (in the range of seconds) that involves the allocation of attention to a particular stimulus/action before the stimulus/action is expected to occur. PA is a prolonged aspect of attention that involves the expectation that a particular target object will occur in a particular location, allowing the anticipation of a target stimulus, and therefore preventing the possible effects of distractors. Maintenance is another prolonged aspect of attention, and refers to the ability to allocate attention towards a particular cognitive activity "for its own sake" (LaBerge, 1995, 1997), without the process of expectation served by PA. In the frame of this theory, the present study is dedicated to the investigation of the preparatory aspect of attention.

Advance preparation for an expected stimulus allows for a faster and more accurate response (Eriksen & Yeh, 1985; LaBerge et al., 2000; Posner, 1980; Siéroff & Auclair, 2007). Therefore, one of the benefits of attention is that subjects can react more quickly to an expected event. Advance knowledge about a target attribute (e.g., its location or shape) can induce a preparatory strategy in anticipation of the upcoming target (LaBerge, 1995; Posner, 1980). The maintenance of an active attentional preparation over time requires a mental representation of a target stimulus to be stored in working memory during the time of preparation. The mental representation of the expected event starts the perceptual processing of that event, speeding the perception of the stimulus when it is actually presented (pre-perception).

When individuals prepare for an upcoming stimulus, attention is trigged endogenously, as it is shaped by intentions or goals coming from the observers mind (Corbetta & Shulman, 2002). In endogenous or voluntary attention, the control is exerted in a top-down manner and is affected by subject's expectations and by current goals stored in working memory (Jonides, 1981; Posner, Snyder, & Davidson, 1980). Attention can also be triggered exogenously by an event coming from the environment. However, in exogenous attention the control is exerted in a bottom-up manner, by sensory stimulation, and is not affected by subjects' expectations, contrary to the voluntary control of attention.

As the amount of PA is influenced by internal expectations of a particular stimulus (LaBerge et al., 2000), PA should be affected by factors that modulate expectations. Internal expectations of a certain stimulus can be modulated by changing its global probability or predictability, in spatial or temporal dimensions, or by having preliminary information about some aspect of that stimulus, introduced by specific pre-cues or instructions (Jentzsch &

Sommer, 2002; Matt, Leuthold, & Sommer, 1992). Therefore, the amount of PA directed to an expected stimulus can vary according to different characteristics of that stimulus and the context in which is expected to occur.

1.2. PA and the effect of stimulus probability

Increasing a particular stimulus probability increases the predictability of that stimulus, and thus its certainty. As a consequence, the intensity of PA directed to the expected stimulus should be modulated by the degree of certainty of the occurrence of that event in the near future.

It has been widely demonstrated that augmenting the global frequency of a stimulus appearance speeds the processing of that stimulus and its corresponding response. That is to say, the frequency of a stimulus occurrence has a negative correlation with the time taken to respond (Bertelson & Tisseyre, 1966; Hyman, 1953). LaBerge and Tweedy (1964), studied the effects of stimuli probability in the behavioral performance of human subjects, while controlling the effects of response probability. In their experiments, subjects were instructed to make a motor response by pressing a button when a certain stimulus was presented (e.g. green square) and to make a second response when either of two other stimuli were presented (e.g. red or blue square). They varied the presentation ratio of the red and the blue stimuli to 1:5 reasoning that, since both stimuli were associated to the same response, any differences in response times (RTs) should be attributable to changes in stimulus probability. Indeed, they found that subjects responded faster to the more frequent stimulus, even though they elicited the same response. This finding is in agreement with the assumption that the amount of PA to the perception of a particular stimulus increases when the relative frequency of its appearance also increases. Therefore, the certainty of an event's occurrence might modulate the intensity of PA directed to it.

In another sequence of studies using a similar two-choice speeded identification task (two stimuli associated with one response and a third stimulus associated with the other response), LaBerge, Legrand, and Hobbie (1969) showed that PA directed to one of the stimuli associated with the same response can be reinforced by adding a positive feedback after a correct response to that stimulus. This finding suggests that PA can be regulated by

motivational factors, a basic assumption in the top-down or voluntary modulation of attentional control.

The influential effect of event frequency in PA has also been tested using the *spatial cueing paradigm*. The spatial cueing paradigm has been a useful tool to examine the processes taking place when one directs attention to a peripheral visual location and the forthcoming processing of the information in that visual space. In spatial cueing studies (Posner, 1980), participants are instructed to fix their vision on a central item (e.g. a central dot), and to respond to a pre-cued visual target (e.g. an asterisk) presented in one of two peripheral locations. The cue can be an increase in the size and/or the brightness of one of the peripheral boxes. Studies using this paradigm manipulated the validity of the spatial visual cues, with validity defined as the relationship between the cue and the target locations (see Fig. 2). There are valid trials (the cue indicates the target location), invalid trials (the cue indicates a different location than the target), and neutral trials (both or neither locations are signaled). The time taken to respond to a target in the cued location (benefit = valid cue trials - neutral trials) is compared to the time taken to respond to a target in an uncued location (cost = invalid cue trials - neutral trials). The usual finding is that it takes less time to respond to a target presented at the cued location and more time to respond to a target presented at an uncued location, compared to a neutral condition. In other words, when attention is allocated to a specific region in space (engagement) there is a benefit in the forthcoming information processing at that location. Conversely, there is a cost in directing attention to a different location in visual space to process the relevant target information (disengagement).

The attentional activity allocated to a particular region in visual space before the stimulus occurrence can be modulated by the predictability of the cue. The cue can capture subjects' attention in an exogenous or bottom-up manner when it is non-predictive, i.e. non-informative of the target location (equal probability of valid and invalid trials). Observers cannot ignore the cue and they passively allocate attention to the cued location, in response to the sudden salient stimulus. This passive capture of attention can be differentiated from the voluntary allocation of attention. When the cue is predictive (informative) of the target location, subjects can direct attention to that location in an endogenous or top-down manner. After an informative cue, subjects can strategically control the allocation of attention. For instance, if the target appears in the location indicated by the cue (valid) in 80% of the trials and the target appears in an uncued location (invalid trials) in 20% of the trials, the predictive value of the cue encourages subjects to voluntarily attend to the cued location (Jonides, 1981).

Besides, if invalid trials are more frequent than valid trials (e.g. 80% of invalid trials and 20% of valid trials), attention can be voluntarily directed away from the cue location (Bartolomeo, Siéroff, Decaix, & Chokron, 2001; Couette, Bachoud-Levi, Brugieres, Siéroff, & Bartolomeo, 2008; Danckert, Maruff, Crowe, & Currie, 1998; Maruff & Currie, 1995; Posner, Cohen, & Rafal, 1982). In this counter-predictive cue condition (greater proportion of invalid than valid trials), responses are faster for invalid than for valid trials, suggesting that subjects take into consideration the location in which the target is more probable to appear. Hence, the predictive force of the cue and target combination is crucial in encouraging subjects to voluntarily attend towards or away from the cued location.

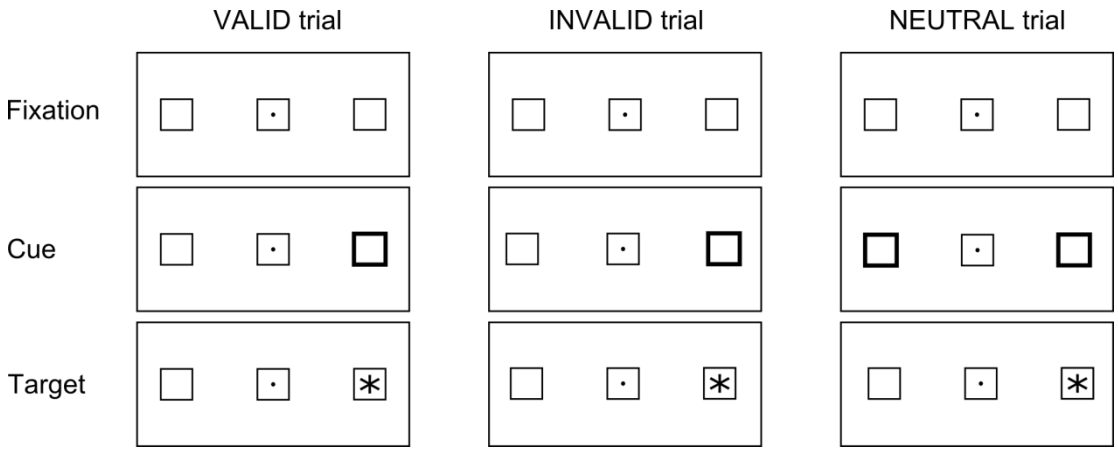

Figure 2. Schematic illustration of valid, invalid, and neutral trials in a typical spatial cueing task with peripheral cues.

1.2.1. *Probability effect as a consequence of the strategic allocation of PA*

Individuals can develop different strategies in preparation for the occurrence of an expected event. As mentioned in the previous section, the attentional resources directed to a spatial location before a target occurrence can be modulated by a spatial cue. Jonides (1980) has proposed a model for the operation of attention in tasks with less than 100% of validly cued trials. He claimed that in such tasks subjects use a *probability* or *frequency matching* strategy (Jonides, 1980, 1983). This strategy consists in allocating attentional resources towards the cue location according to the likelihood that this location will contain a target (cue predictability). This means that subjects match the proportion of trials in which the cued position has a high priority for resource allocation with the predictability of the cue.

Increasing the cue predictability increases the proportion of trials in which the cued position has a high priority for resource allocation. In contrast to the *frequency matching* strategy, there is another possible strategy for allocating attentional resources in spatial cueing tasks. This strategy consist of systematically directing high attentional resources to the most probable event (Van der Heijden, 1989), a strategy known as *maximizing*. For instance, in a condition with 80% of validly cued trials, *maximizing* implies the allocation of greater attentional resources towards the cued location in *every* trial.

The voluntary distribution of attention according to the expected probability of the target at the cue location has been demonstrated in adults' research with predictive spatial cues. These studies suggest that human adults distribute attentional resources in visual space according to the most probable location in which a target could occur, and somewhat, to the less probable location, noticing that some trials are invalid (*frequency matching*). Interestingly, research in children using predictive spatial cues shows that at very young age (6 years old) they have a larger advantage (faster RTs) of valid over invalid cues than older children and adults (Leclercq & Siéroff, 2013; Wainwright & Bryson, 2002). This result suggests that very young children may not take into account the probability of invalid cues and they might direct attention only to the most probable location. In other words, young children may maximize the attention directed to the cue location, even though the cue is invalid in a proportion of trials. Contrary to older children and adults, younger children may have difficulties in controlling the distribution of attention according to the probability of events. These results suggest that the ability to voluntarily distribute (modulate) attention in space as a function of probabilities gradually develops with age, contrary to the exogenous or involuntary capture of attention that is already present at very early ages.

Traditionally, the implementation of the *frequency matching* and *maximizing* strategy was examined using the two-choice prediction task, known also as guessing task (Yellott, 1969). In a typical guessing task, subjects are asked to predict (guess) in each trial which of two possible events will be displayed in the near future. For instance, in an experiment used by Yellott (1969), subjects had to predict which of two letters, "X" or "Y", would appear in a display window. At the beginning of each trial the participant made his prediction by pressing one of two keys (the choice) and then one of the letters was presented (the outcome). If the letter presented coincided with the participant choice, this was counted as a correct outcome. Each choice had different probability to produce the correct outcome e.g. the first choice had 80% probability and the second choice had 20% probability. In guessing tasks, participants

can exhibit a *frequency matching* strategy. This strategy consists of choosing the first option 80% of the time and the second option 20% of the time. The *frequency matching* strategy is not the most optimal one in this type of tasks, as it leads to a correct outcome in only 68% of choices (0.8*0.8+0.2*0.2). The most optimal strategy is *maximizing*, which consists in systematically chose the option with more probability to produce the correct outcome. *Maximizing* leads to a correct outcome in 80% of trials (0.8*1.0+0.2*0.0).

Even though *maximizing* is the most optimal strategy under uncertainty (when the sequences of events are random), human adults tend to match the frequency of events (Estes, 1976; Vulkan, 2000; Yellott, 1969). Developmental studies using the guessing task have shown that very young children (3 to 6 years old) tend to choose the option that has occurred most frequently in the past, that is, they use a *maximizing* strategy (Derks & Paclisanu, 1967; Jones & Liverant, 1960). This result suggests that the *frequency matching* strategy develops with age, in line with the results obtained in young children using the spatial cuing paradigm. Furthermore, it is interesting to ascertain that whereas the *frequency matching* strategy is not generally found in other species, animals do tend to maximize in the same conditions (Hinson & Staddon, 1983). The fact that humans adults tend to match the frequency of events in an uncertain context led researchers to relate the *frequency matching* strategy to the human capacities of interpreting reality searching for patterns under uncertainty and of testing hypothetical rules (Gaissmaier & Schooler, 2008; Wolford, Newman, Miller, & Wig, 2004). These capacities are presumably not well developed in young children or other animals. It can be argued that, by predicting the next event in the near future, participants may also induce a preparatory state before the stimulus arrival. In the act of predicting the future event in guessing studies, subjects may control the allocation of PA to one stimulus or the other. Thus, the results of these studies can also be related to the human capacity to strategically distribute attention to the upcoming event, taking into account their relative frequency in the past.

1.2.2. *Alternative explanations to probability effects*

The behavioral benefit (faster RTs) of allocating PA to an event as a function of its probability in the past is related to the strategic control of the distribution of visual attention before the event's occurrence. Apart from this strategic explanation, there are several

alternative explanations for the effect of events' frequency on behavior. In the next section, we will be briefly present two of them.

1.2.2.1. The automatic-activation account

The behavioral benefit to responding to targets that are more likely to occur can also be explained by the automatic preactivation of neuronal networks when the repetition of specific stimulus or event increases in the sequence of trials (Lamb, London, Pond, & Whitt, 1998). According to the automatic-activation account, the efficiency and speed of the analysis of a certain type of information results from the prior activation of the information-specific neural mechanism. The identification of a certain type of information in a given trial activates the appropriate information-specific mechanism, and the identification of the same type of information in subsequent trials is facilitated due to the prior activation of the appropriate neural mechanism. The neural specific activation would increase gradually as the number of trial repetitions increases. Such neural activation is an automatic process that is not under voluntary control and cannot be suppressed voluntarily.

The automatic-activation account proposes that the probability effect found in studies that manipulate the frequency of stimuli can be explained by the increase in stimuli repetition rather than by strategic process. Increasing the frequency of a given stimulus increases the likelihood that it will be repeated. As a consequence, RTs are faster to more frequently repeated stimuli (stimuli with higher probability) than to non-repeated or less frequently repeated stimuli (stimuli with lower probability).

This automatic hypothesis does not rule out the possibility that controlled mechanisms might operate under some other conditions. For instance, in experiments in which participants receive a cue before each trial indicating which level would contain the target, the performance varied depending on the cue-validity condition (Robertson, Egly, Lamb, & Kerth, 1993). In the experiments of Robertson et al. the level of repetition for the different cue-validity conditions was presumably equal. Therefore, the automatic-activation account does not eliminate a possible controlled process underlying the probability effect in some experimental conditions, such as when a cue anticipates the probable target level.

1.2.2.2. The compound-cue frequency account

This account is based on the theoretical ideas developed in the framework of memory retrieval studies. According to the compound cue theories of memory retrieval, the cue used to access memory is a combination of the target memory and the contextual information used for retrieval (e.g. semantic cue). For instance, in a semantic priming experiment in which a participant is shown the prime word *scissors* followed by a target word *cut*, the compound cue *scissors-cut* is used to access memory (Ratcliff & McKoon, 1988). The assembly of the compound cue in short-term memory is the result of automatic processes.

In the context of the spatial cueing paradigm, it has been proposed that the cue and the target events can act as a *compound cue* (Risko, Blais, Stolz, & Besner, 2008). The cue-target combination, rather than the single cue, may facilitate the retrieval of an associated response. For example, if the target (T) is preceded by a spatial cue in one of two locations (e.g. L1 and L2), the compound cue formed by T+L1 or T+L2, rather than the single cue (L1 or L2) would be used to retrieve a response from memory.

If the cue-target combination is used as a compound cue for memory retrieval, the frequency with which a given cue-target event occurs should influence performance. Increasing the frequency of cue-target events should increase the ease of retrieval, decreasing the time taken to respond. In spatial cueing studies, when the proportion of a valid compound cue (e.g. spatial cue + target appearing at the same location) is high, RTs to these trials are faster. In the same line, when the proportion of invalid compound cue (e.g. spatial cue + target appearing at the opposite location) is low, RTs to these trials are slower. Thus, according to the compound-cue frequency account, the decrease in RTs for valid trials and the increase in RTs for invalid trials simply reflect the consequence of the well-documented effect of events frequency claiming that responses are faster to frequent than to infrequent events (Bertelson & Tisseyre, 1966; Hyman, 1953). This means that the probability effect found in spatial cueing paradigms with predictive cues might be the consequence of automatic processes.

The compound cue account may explain the results of the effect of cued trials proportion only in certain conditions. Specifically, in the study of Risko et al. (2008) the time interval between the cue and the target presentation was short (150ms). However, the voluntary allocation of attention is known to be a slower process (see next section). Therefore, the compound cue account does not rule out the idea that the proportion cue effect is the consequence of controlled processes under some experimental conditions, such as when the

temporal interval between the cue and the target are long enough to engage controlled processes.

1.3. PA and time

In the previous section we described studies suggesting that the predictability of a target in a spatial region modulates the voluntary distribution of attention in the visual field. However, the spatial location of the target event is not the only target characteristic that was shown to have an effect on attentional processes. The temporal characteristic of the target presentation is another crucial aspect that influences attention.

Since early studies on attention, researchers have been interested in the effect of time. The allocation of attention to a relevant target was shown to have time constraints. For instance, when subjects have to respond to the appearance of two signals presented in rapid succession, the RT to the second signal depends on the delay between the first and the second signal (so-called *stimulus onset asynchrony* or SOA). In this context, participants respond faster to the second event when the delay between the two stimuli is larger, than when a short delay separated them (for an early review see Smith, 1967).

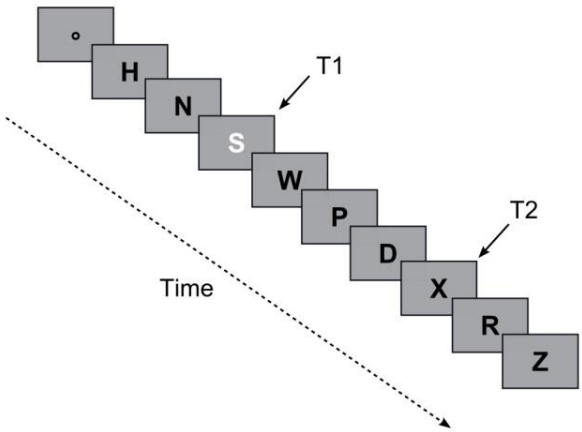

Figure 3. Illustration of the rapid serial visual presentation task. Participants monitor a rapid visual sequence for two different targets. For example, target 1(T1) might be a white letter in a black string and target 2 (T2) might be the letter X (See text for details).

The task usually used to study the constraints of attention allocation over time is the rapid serial visual presentation (RSVP) task, in which successive targets are presented in a rapid sequence (Broadbent & Broadbent, 1987; Chun & Potter, 1995). In this task, participants are required to monitor a stream of stimuli, usually letters, and to respond as soon as they detect a target (Fig. 3). The target is usually differentiated from non-targets by color. The stream of letters is presented at a rate of about 100 ms per item, all at the same location. Usually, the pattern of results shows that attentional processing for items that follow the target is impaired between 200 and 500 ms. This means that a second target (T2) appearing between 200 and 500 ms after the presentation of target 1 (T1), is likely to be missed. This phenomenon is known as the *attentional blink* effect (Raymond, Shapiro, & Arnell, 1992), and is in accordance with the assumption that attention requires a certain amount of time be allocated to a target stimulus.

The time required in attentional processing may depend on whether attention is voluntarily or involuntarily directed to a target and on the task demands. The voluntary or endogenous allocation of attention to a visual stimulus is a slow and relatively long lasting process. In contrast, the involuntary or exogenous allocation of attention was demonstrated to be a faster process with a rapid decay over time.

The time course and properties of voluntary and involuntary allocation of attention heve been widely studied using the spatial cueing paradigm (Müller & Rabbitt, 1989; Posner & Snyder, 1975). In spatial cueing studies, the cost or benefit of the cue was shown to depend on the cue predictive value and on SOA, that is, on the temporal delay between the cue presentation and the target appearance (see Fig. 4). When the cue is predictive and attention is allocated voluntarily, the benefit in RTs increases as the SOA gets longer. The benefits of voluntary attention only appear between 350 and 500 ms after the cue presentation, reaching to a maximal level for SOAs between 800 and 1000 ms (Müller & Rabbitt, 1989). This means that voluntary attention takes a certain time to develop, but once it is directed to a spatial location, its effect can be sustained over time (Posner et al., 1982). In contrast, when the cue is non-predictive, and attention is involuntarily directed to the cued location, the benefit in RTs is larger at short SOAs (50-100 ms) and decreases as SOA gets longer. More precisely, when SOA is longer than 300 ms, the target RT is slowed down at the cued location and is faster at the non-cued location (Posner & Cohen, 1984), resulting in faster RTs on invalidly cued trials. This phenomenon is known in the literature as *inhibition of return* and it has been related to an automatic mechanism that helps individuals to explore the visual environment,

by avoiding repeated processing of the same location (Klein, 2000). Thus, involuntary allocation of attention acts faster than voluntary attention, but is less persistent over time.

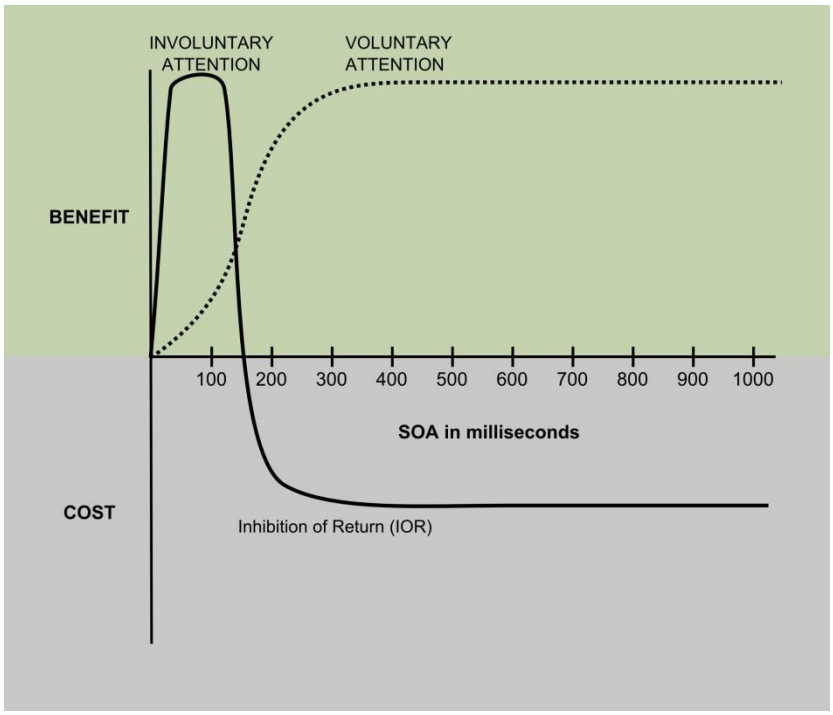

Figure 4. Differential cost and benefits of involuntary and voluntary allocation of attention as a function of stimulus onset asynchrony (SOA). Modified from Bartolomeo and Chokron (2002).

In summary, the time required to efficiently process a target varies with the task demands and the probability context in which the target is expected to occur. The voluntary allocation of attention to a target event prior to its occurrence is a slow process that can be trigged by the high predictability of the target in a specific spatial location. This means that PA is not a static operation but a dynamic process depending on the spatial and temporal framework in which stimuli are embedded.

1.3.1. *Allocating PA to a point in time*

In spatial cueing paradigms, predictive cues give information about the target probable location, allowing subjects to voluntarily direct attention toward the cued location in anticipation of the upcoming target. Allocating attention to the spatial location in which a

target is expected to occur improves further target processing in that location of the visual field. The dynamics of attentional operations in the spatial and the temporal dimensions raise the question of whether anticipating the point in time in which a target stimulus occurs also improves its subsequent processing.

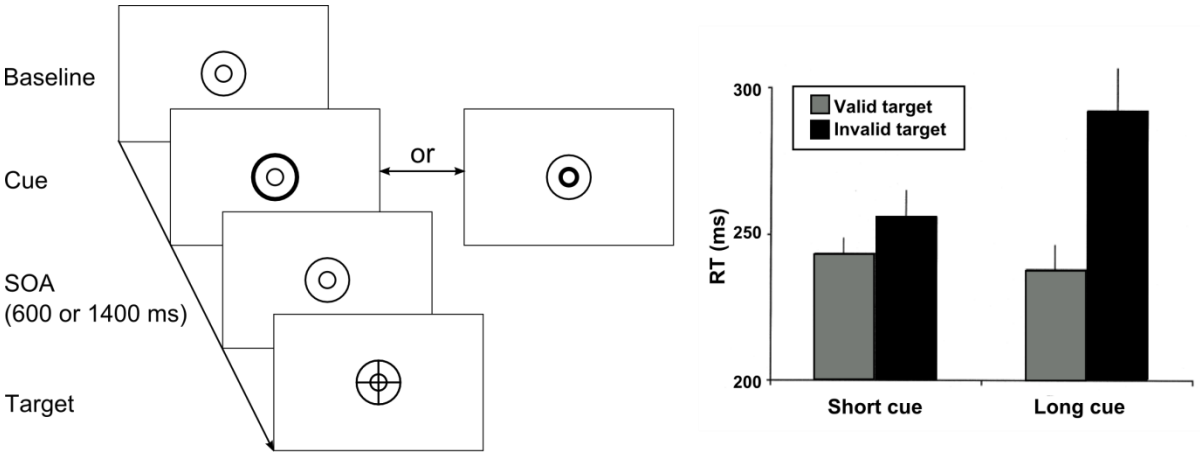

Figure 5. Illustration of the behavioral task (left) and corresponding reaction-time results (right) from the temporal attention orienting task used by Coull et al. (2000). A central symbolic cue (brightening of inner or outer circle) indicated the likely interval (short = 600 or long = 1400 ms stimulus onset asynchrony, SOA) after which the target would appear with 80% validity. Targets (cross) appeared briefly and required a simple detection response. Subjects detected validly predicted targets significantly faster than unexpected (invalid) targets. This effect was larger for targets appearing at a short SOA than for targets appearing at a long SOA (see text for details).

The information about the point in time at which a certain stimulus occurs can modulate internal expectations and can be used dynamically to optimize behavior. The influence of temporal information about a target appearance in subjects' expectations has been investigated using a temporal version of the spatial cueing paradigm. The *temporal attention orienting task* allows the examination of behavioral benefits and/or costs of voluntarily directing attention to a specific point in time (Nobre, 2001; Coull & Nobre, 1998; Miniussi, Wilding, Coull, & Nobre, 1999). In studies using this task, subjects were instructed to respond to a foveally presented target (e.g. a cross) preceded by one of two possible symbolic cues (see Fig. 5 for a display example). The cues were also foveally presented (e.g. luminance of concentric circles) and indicated the probable delay at which a particular target event would appear within a trial. The cue validly indicated (e.g. 80% of valid trials) that the target would appear at a short SOA (e.g. 600 ms) or at a long SOA (e.g. 1400 ms). This means

that cues were predictive about the moment in time in which the target would appear. In the remaining trials (e.g. 20% of trials), the cue invalidly indicated the target SOA. There were two types of invalid trials: invalid trials with a cue indicating a short SOA and invalid trials with a cue indicated a long SOA. After an invalid cue indicating a short SOA the target appeared later than the cued delay, and after an invalid cue indicating a long SOA the target appeared earlier than the cued delay.

A series of experiments using the *temporal attention orienting task* have shown that RTs were faster when the delay of the target appearance was validly cued than when it was invalidly cued. The benefit in RTs of valid trials provided evidence that subjects were able to use the temporal cue to effectively allocate attention to a specific moment in time, in which targets were shown to be processed more quickly (Coull & Nobre, 1998) and accurately (Davranche, Nazarian, Vidal, & Coull, 2011). Interestingly, the behavioral cost after an invalidly cued trial depended on the SOA indicated by the cue. There was a larger cost in RTs after an invalid cue indicating a long SOA than after an invalid cue indicating a short SOA. This means that there was a larger cost in allocating attention earlier than indicated by the cue rather than in allocating attention later than indicated by the cue. It was suggested that after an invalid cue indicating long SOA, the sudden appearance of the target might produce a substantial cost, because subjects did not expect the target at that point in time. In contrast, after an invalid cue indicating short SOA, and following the non-appearance of the target stimulus at a short SOA, subjects might voluntarily prolong their attention to the later SOA, reducing the behavioral cost in this type of invalid trials. Attention might be prolonged to the longer SOA because the target always occurred within a trial. Therefore, we might also suggest from this finding that the reduced behavioral cost for invalidly-cued targets appearing later than indicated by the cue was the consequence of the higher probability of the target occurrence at the long SOA. Thus, the voluntary preparation of subjects may have been modulated by the temporal probability of the target occurrence within a trial.

1.3.2. *PA and stimuli temporal probability*

The influence of a stimulus temporal probability on the voluntary allocation of attention has been studied in paradigms that varied the probability of a stimulus presentation within a trial. The result of studies in which the target can appear at different SOAs with equal

frequency (equal *a priori* probability) showed that RTs to the target stimulus decrease with increasing SOA length (Niemi & Näätänen, 1981; Woodrow, 1914). For instance, in an experiment in which two SOAs are used with equal frequency, the probability of the presentation of the target after each of the two SOAs is initially .50. After the first SOA has passed the target occurs at the longer SOA with a probability of 1.0. The phenomenon of obtaining faster RTs as SOA gets longer was generally associated with the increase of the conditional (*a posteriori*) probability of the stimulus as time passes, increasing its certainty in time. It was proposed that the number of remaining SOAs in which a target can occur decreases as time passes during a trial ("aging" SOAs), and therefore the probability of the target occurrence in the next possible SOA increases. Thus, at the longer SOA, participants may reinforce their preparation to the target given its high probability of appearance. This proposal was tested in experiments using non-aging SOAs, that is, in experiments that maintain the same *a posteriori* probability of the target occurrence in each SOA. Continuing with the example of an experiment with two possible SOAs, non-aging SOA implies that the probability of presentation of the target in the first SOA is, for example, .50. After the first SOA has passed the target occurs at the second SOA with a probability .50, and therefore there is the same conditional probability of the target occurrence at each SOA. In experiments using non-aging SOAs, RTs to the target remained constant across all possible SOAs (Niemi & Näätänen, 1981; Trillenberg, Verleger, Wascher, Wauschkuhn, & Wessel, 2000). Altogether, these results show that the temporal probability of a target stimulus within a trial influences its temporal predictability or certainty, and consequently it influences the preparation to a target appearance at a specific point in time.

The increase in the speed and effectiveness of processing a target with high temporal probability was also demonstrated in a discrimination task (Wagener & Hoffmann, 2010). In a recent study, Wagener and Hoffmann presented to participants two target objects that could appear either at a short (600 ms) or a long (1400 ms) SOA. One target was more frequently presented at one SOA and the other was more frequently presented at the other SOA. The targets were displayed in the center of the screen. Authors reported that subjects responded faster and more accurately to each target at the SOA in which it was more probable to occur. In another experiment from the same study, targets could appear in two different locations. The probability of a target appearance in each location at short or long SOAs was manipulated. Precisely, the target appeared more frequently in one location at the short SOA and in the other location at the long SOA. The results of this experiment showed that subjects

responded faster and more accurately to the most probable distribution in space and time. This finding demonstrated that the temporal probability of the target interacted with its spatial probability to increase the speed and efficiency of stimulus processing.

In summary, the results of studies manipulating the temporal probability of events suggest that the amount of PA directed to a target stimulus is also modulated by the temporal predictability of that stimulus.

1.4. PA and task difficulty

The presentation of targets with distracting information may lead to perceptual interference and/or response conflict, increasing the difficulty in a given task. In difficult situations more attentional control is needed to correctly respond to a target, overcoming the influence of distracting information.

Different aspects of the stimulus display might increase the difficulty, and thus the attentional demands, in a given task. A well-documented factor that influences the difficulty in attentional selection is the similarity between relevant and irrelevant information. The interference of a distractor increases as the target-distractor similarity increases, slowing the processing of the target information (Eriksen & Eriksen, 1974). The selection of a target also increases in difficulty when it is located in close spatial and/or temporal proximity to irrelevant distractors. In relation to spatial proximity, decreasing the distance of distractors from the spatial location in which a target is expected to appear was demonstrated to increase the RT to that target (Eriksen & St. James, 1986). This behavioral cost has been associated with the interference of distractor as it gets spatially closer to the target. Also, the temporal proximity between targets and distractors has been associated with selection interference.

The most documented constraint in selecting a target appearing in close temporal proximity to distractors is the *attentional blink* phenomenon, presented in the section entitled "PA and time" of the present Chapter. Several studies using the RSVP task (Fig. 3) argued that the failure in the efficient inhibition of distractors located in close temporal proximity to the target contributes to the *attentional blink* effect (e.g. Dux & Harris, 2007). Increasing the

temporal proximity between relevant and irrelevant information might increase the effect of distracting information, making more difficult to select the target (Jiang & Chun, 2001).

The presence of competing distractor information was shown to impair the selection of relevant target information. However, the ability to select a target in difficult situations was demonstrated to be influenced by the expectation of distractor information. In other words, when distractors are also expected in an upcoming task, this expectation can be strategically used to adapt the behavior accordingly. Subjects might use this information to voluntarily increase the amount of attention directed to the relevant target information prior to its occurrence, or to voluntarily suppress the attentional activity directed to distractors, or to do both. Thus, anticipating the perceptual and/or response difficulty in a given task might allow subjects to develop a preparatory strategy to respond to the attentional demands of the task at hand.

1.4.1. *The strategic control of attention under difficulty*

Several behavioral tasks have been proposed in the literature to study the control of attention in difficult situations (Fig.6). In these tasks the influence of irrelevant distracting information on the selection of relevant target information is examined. In the Stroop task (1935), for example, the subject is asked to name the font color (relevant information) in which a color word (irrelevant information) is printed. There are two types of trials: congruent trials, in which the font color and the printed word are the same (e.g. the word *green* printed in green ink), and incongruent trials, in which the font color is different from the word itself (e.g. the word *green* printed in red ink). The general result of experiments using the Stroop task is that responses are slower in incongruent compared to congruent trials. Eriksen & Eriksen (1974) developed a similar paradigm in which a target (relevant information) is presented simultaneously with distractors (irrelevant information), known as the flanker task. Subjects had to make a discrimination judgment of the central letter (target) in a row of seven. Two different sets of letters were mapped with two different responses (H and K with one response *vs* S and C with another response). In congruent trials, the distractors were associated with the same manual response as the target. In incongruent trials, the distractors were associated with the alternative response. The usual result with the flanker task is that RTs are slower in incongruent that in congruent trials.

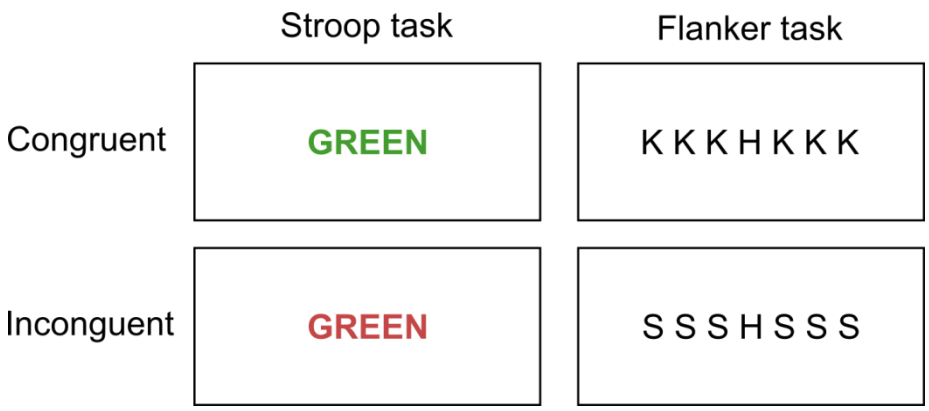

Figure 6. Schematic illustration of congruent and incongruent conditions in the Stroop and the flanker tasks (see text for details).

The presence of incongruent distracting information in the Stroop and the flanker tasks increases the difficulty to select the relevant information, taking more time to respond. However, the interference between relevant and irrelevant information in these tasks can be modulated and strategically controlled. Logan & Zbrodoff (1979) reported that the interference of the irrelevant information in a version of the Stroop task can vary as the relative frequency of congruent and incongruent trials varied. When incongruent trials were more frequent than congruent ones, RTs to incongruent trials were faster, reversing the usual Stroop effect. In this condition, the frequency of incongruent trials increased, increasing the probability of distracting information. Therefore, subjects presumably adopted a strategy taking into account the predictive information in the frequency manipulation.

The strategic use of the information on the probability of incongruent distractors was also demonstrated with the flanker task. Gratton, Coles and Donchin (1992) showed that the interference of irrelevant information in a flanker task can be modulated by observers' expectancy: increasing the probability of incongruent irrelevant information decreases the cost in RTs between incongruent and congruent trials. In another experiment, Gratton et al. manipulated subjects' expectancies in a trial-by-trial manner. At the beginning of each trial, a symbolic cue was presented indicating the level of interference in the upcoming trial (low interference for congruent trials and high interference for incongruent trials). They found that anticipating the upcoming level of interference by means of a cue decreased the cost in RTs between incongruent and congruent trials. The cue might have warned subjects about the

attentional demands in the forthcoming trial, allowing a strategic adjustment of attention to adapt current behavior.

To conclude, the information arising from distractor probability can be strategically used to control the allocation of attention to a target event in a difficult task. The anticipation of distractors may influence the distribution of attention towards targets/distractors in preparation to their appearance.

1.4.2. *The spatial distribution of PA according to expected distractor interference*

Some studies examined the question of whether attention can be strategically distributed in the visual field in relation to the expected distractor interference. In a modified version of the Stroop task, Crump, Gong, and Milliken (2006) investigated the ability of the human cognitive system to use contextual information for adjusting the allocation of attention. They asked participants to classify the color of rectangles that were presented either above or below the center of the screen. Each rectangle was preceded by a color word, which could match (congruent) or not (incongruent) the color to be named. Authors varied the proportion of congruent trials relative to incongruent ones in a location-specific manner: one location was associated with a high probability of congruency between the word and the color shape, and the other location was associated with a low probability of congruency. Thus, the spatial context indicated whether an item was probably congruent or incongruent. If attentional resources were strategically distributed in the visual field according to spatial probabilities of congruency there should be less interference in a location in which incongruent information is highly expected comparing to a location in which the expectation of incongruent information is lower. In accordance with this hypothesis, Crump et al. found that the interference of irrelevant information was significantly reduced in the location with high frequency of incongruent items compared to the location with low incongruent frequency. Hence, the context-related expectation of difficulty (e.g. distractor spatial probability) might modulate the strategic allocation of attentional resources in different regions of the visual field (Corballis & Gratton, 2003; Wendt, Kluwe, & Vietze, 2008).

In summary, PA directed to relevant target information might also be modulated by the expected probability of distracting information. Increasing the probability of distractors' interference presumably increases the amount of attentional control necessary to respond to the target. Anticipating the difficulty in a given task might allow for the development of a preparatory strategy to distribute attentional resources according to the expected demands.

1.5. Conclusion

PA is a crucial manifestation of attentional control that allows subjects to react more quickly and more efficiently to an expected event presented in the environment. The attentional activity directed to the processing of a stimulus prior to its occurrence seems to be highly influenced by different properties of the expected stimulus and its context. Preliminary information about some aspect of the expected stimulus, introduced by specific pre-cues or instructions, or by changing the stimulus probability, might modulate PA. Increasing the probability or certainty of that stimulus in spatial and temporal dimensions increases the speed and accuracy of the stimulus processing. This means that the information arising from the spatial and temporal probability of a relevant stimulus can be used strategically to distribute PA. In difficult situations, in which more attentional control is necessary to select a relevant target from distracting information, the probability of distractors might also influence PA. The information arising from distractors' probability may be used to develop a preparatory strategy in response to the expected attentional demands of the task. Thus, the influence of the expected stimuli probability on subject's behavior might be the consequence of the strategic distribution of PA in relation to such probabilities.

CHAPTER 2: Preparatory attention and the brain

Attention is an essential cognitive ability to effectively process the information from our environment. A variety of experiments using behavioral measures was presented in Chapter 1. They described the behavioral advantages of allocating attention to an expected stimulus. Cognitive neuroscience has been traditionally interested in the relationship between brain and behavior, and elucidating the neural bases of attentional processes continues to be a key challenge in neuroscience research (Mangun, 2012).

2.1. Common methods in cognitive neuroscience to study the cerebral bases of visual attention

There are many different methods of analyzing the brain during attentional demanding tasks. They give the opportunity to have an overview of the relationship between neural activity and attentive behavior. In the next paragraphs, the most common methods used in cognitive neuroscience to study the cerebral bases of visual attention will be briefly presented. With the goal of being illustrative rather than exhaustive, advantages and constraints of each method will be described, as well as some findings and implications in PA.

2.1.1. *Brain lesion method*

Studies of neuropsychological patients have made important contributions to the understanding of the relationship between brain and behavior. When a particular brain region is damaged, behavioral changes or interference in the performance of a specific task occur. As a consequence, the damaged region can be correlated with a deficit in the cognitive operation necessary to correctly execute the task. Thus, the brain lesion method allows for the testing of hypotheses concerning the role of a damaged brain region in tasks demanding attentional processing.

Different attentional deficits were observed after frontal and parietal damage. For instance, damage in the posterior areas of the parietal lobe has been shown to impair the ability to orient attention in the visual field, suggesting a crucial role of the parietal cortex in visual orienting of attention (Posner, Walker, Friedrich, & Rafal, 1984). Damage in the prefrontal cortex (PFC) harms the ability of individuals to control and regulate the attention directed to a relevant visual stimulus (Swick & Knight, 1998). In difficult situations, attentional control might be necessary to select the relevant information from irrelevant noise. Patients with frontal damage are impaired in selecting relevant targets when concomitantly presented with irrelevant distractors, demonstrating the crucial role of the frontal lobes in attentional control (Richer et al., 1993). Frontal lesions also affect the capacity to maintain attention toward an expected stimulus prior to its occurrence (Stuss et al., 2005). The representation (mental image) of a target stimulus must be stored in working memory to maintain an active attentional preparation during the time interval before a target occurrence. Patients with frontal damage are impaired in tasks demanding working memory processing (Owen, Downes, Sahakian, Polkey, & Robbins, 1990), suggesting that frontal areas are essential in the capacity of withholding a mental representation of an expected event.

The findings of studies on neurological patients provided relevant insights into the relationship between brain regions and attentive behavior. They show, for instance, that frontal and parietal areas are particularly involved in visual attention. However, the lesion method has several limitations with respect to the possibility of making inferences about the human normal cognitive function. A lesion in the brain can disrupt the cognitive system in a variety of ways, specifically because it may differ in size and origin (etiology) between patients. The compensatory effects of lesions on brain and behavior are another important issue to take into account after neurological damage. It has been demonstrated that the neural circuits recruited for a specific cognitive task can change after brain damage. This means that the recruitment of some preferential brain pathway in normal brain functioning can be compensated by passing information through other pathways when the preferential one is damaged (Swick & Knight, 1998). Hence, as the study of patients with brain damage consist in the study of an abnormal brain, it is difficult to make inferences about the true functions of the damaged brain region in a normal population.

2.1.2. *Techniques for modulating the normal brain activity: "virtual lesions"*

Transcranial magnetic stimulation (TMS) is a non-invasive procedure that produces a focal stimulation of the brain. TMS consists in delivering a brief and focal magnetic pulse over the scalp to induce a transient electrical current in the underlying brain tissue. As a consequence, the activity of the targeted neuronal populations is modulated during a very brief period of time. TMS can be applied in single pulses or a series of pulses, the latter is known as repetitive TMS, or rTMS. The stimulation of a specific brain area disrupts the normal activity in the selected region, producing an alteration of the firing-patterns of the neurons. Thus, TMS allows the study of the function of the disrupted tissue. Similar to the technique of TMS, the *Transcranial Direct Current Stimulation* (*tDCS)* technique is a non-invasive and painless method of stimulation. The excitability of brain regions is modulated by the application of a weak electrical current. In tDCS the anodal from the cathodal stimulation can be distinguished. Whereas tDCS anodal stimulation causes membrane depolarization and increases neuronal firing rates, thus enhancing cerebral excitability, cathodal stimulation diminishes it. In this way tDCS enables, for example, the stimulation of a particular brain area while simultaneously inhibiting another region.

These techniques are known to produce a "virtual lesion" that modulates the brain's normal activity, giving the possibility to infer causal links between the stimulated region and the studied function (Pascual-Leone, Bartres-Faz, & Keenan, 1999). In other words, with TMS and tDCS we can study the causal role of a particular cortical region for a given behavior in an attentional-demanding task. For example, it has been shown that rTMS over the parietal cortex disrupted the human capacity of directing attention in the visual field (Rushworth, Ellison, & Walsh, 2001). This result suggested that the parietal cortex has a crucial role in visual attention processing, in line with studies on patients with parietal damage. The frontal cortex was shown to be particularly involved in the control of attentional distribution according to stimulus temporal probability. TMS over the dorsolateral prefrontal cortex (DLPFC) disrupted the capacity of humans to respond to a target taking into account its temporal probability (Vallesi, Shallice, & Walsh, 2007). Learning the target probability is essential to develop a preparatory strategy in relation to its expected probability of occurrence. In a tDCS study, the PFC was shown to be involved in a probabilistic learning task. Anodal stimulation over the PFC improved implicit learning of stimulus probability, improving, as a consequence, the ability to strategically use these probabilities to adapt

behavior (Kincses, Antal, Nitsche, Bártfai, & Paulus, 2004). These findings suggest that the frontal cortex might be crucial in the strategic preparation to the target appearance in relation to its expected probability or occurrence. The frequency of a stimulus should be withheld in working memory to respond according to its probability. tDCS anodal stimulation over the DLPFC cortex induces an enhancement of working memory performance, suggesting a critical role of this region in working memory formation (Fregni et al., 2005).

Techniques such as TMS and tDCS allow the investigation of the correlation between the cortical activity of a specific region and the behavioral performance in a given attentional task. For instance, the neural modulation of different frontal and parietal regions during attentional demanding tasks suggests that they might have a particular involvement in visual attention. However, there are some constraints in the use of these techniques in studies with healthy subjects. To date, single pulse TMS appears to be safe when applied to healthy subjects. In contrast, rTMS can cause undesirable and dangerous side effects, such as seizures. Therefore, appropriate safety and ethical guidelines must be followed when this method is used (Wassermann, 1998). Although tDCS has a smaller chance than TMS of causing seizures in the person receiving the stimulation, it might cause some other undesirable side effects including headache, dizziness, nausea, and an itching sensation as well as skin irritation under the electrodes (Nitsche et al., 2008).

2.1.3. *Electrophysiological recording methods*

The *Single-cell recording* method measures the activity of individual neurons, which are presumably implicated in a certain perceptual or cognitive operation. This method allows the investigation of the neural correlates of attention. For instance, single-cell recordings in monkeys have demonstrated that spatial attention enhances neuronal responses in the visual cortex evoked by a single stimulus appearing within the receptive field (e.g. Reynolds, Pasternak, & Desimone, 2000). When multiple stimuli appear within a neuron receptive field, the neuronal response tends to be determined primarily by the target relevant stimulus. This means that selective attention modulates the responses of neurons in cortical visual areas (Chelazzi, Miller, Duncan, & Desimone, 2001; Moran & Desimone, 1985).

The recording of neural activity before a stimulus occurrence can give us information about the neural network underlying PA. Liang, Bressler, Ding, Truccolo, & Nakamura

(2002) recorded *Local Field-Potentials* (LFPs) from electrodes implanted in a macaque monkey to investigate the possible involvement of prefrontal cortex in the top-down anticipatory control of sensory processing. LFPs are generated by neuronal ensembles and contain information about the simultaneous activity of single neurons. In the study of Liang et al. the activity of prefrontal and visual cortical areas was recorded as the monkey performed a visual pattern discrimination task. They found that prefrontal sites participated in a synchronized oscillatory network during stimulus anticipation. The strength (power and coherence) of this pre-stimulus prefrontal network was highly correlated with the amplitude and latency of early visual evoked potentials components in visual cortical areas, and with response time. Neuronal synchronization has been proposed as a mechanism by which a neuronal population in one area, the prefrontal area for example, may increase the effective synaptic gain it exerts on target neurons in another area, such as the visual cortical areas. Thus, the results of this study suggest that the synchronized oscillations of neurons in the prefrontal cortex may be involved in preparatory mechanisms that facilitate subsequent sensory processing in the visual cortex (Liang et al., 2002).

The method consisting of recording neuronal activity provides the highest spatial and temporal resolution compared to other methods in neuroscience. However, it has great limitations such as the fact that it is very invasive, hampering its use in humans, and that only a few neurons can be examined at a given time.

Electroencephalography (EEG) allows the measurement of massed electrical activity through electrodes placed on the scalp. In contrast to *single-cell recordings*, this is a non-invasive method that can be used to assess the neural activity in humans as well as in animals. In addition, it allows simultaneous measurement of many brain areas and neural processes. *Event-related potentials* (ERPs) are electrical recordings linked to the occurrence of a particular event in time. Such an event can be, for example, the presentation of a perceptual stimulus. The sequence of ERP that follows a stimulus event is thought to reflect the sequence of neural processes that is trigged by the onset of the stimulus.

The impact of visual attention at early stages of information processing was demonstrated in different ERPs studies. Magnun and Hillyard (1991) measured the effect of attention in a spatial cueing task with predictive cues. They found that attention directed to a target location indicated by the predictive cue modulated early components of brain electrical activity. They demonstrated that sensory processing of the target event was facilitated at the

cued location, compared to the uncued location, in agreement with studies that only used behavioral measurements.

The ERPs method also gives a unique opportunity to measure the brain activity elicited before the appearance of an expected target stimulus as it provides a continuous measure of processing. Electrophysiological studies in humans have found the presence of a negative wave in the time interval between the presentation of the warning stimulus and the target stimulus. This brain potential has been called the contingent negative variation (CNV) because it is a slowly changing, negative-going potential that is dependent on the perception of a contingency between warning and response stimuli. The CNV is thus considered an index of PA (Douros, Karrer, & Rosenfeld, 1987; Padilla, Wood, Hale, & Knight, 2006). The CNV has two components; the early wave is related to the warning signal and the later wave is related to the preparation of the target perception and of the movement to be made following the target stimulus.

In order to separate experimentally the perceptual and motor aspects of PA, Brunia and Damen (1988) have proposed a clever task. They used a time estimation paradigm, where subjects had to press a button after an estimation of a fixed time interval. Following 2000 ms of the movement execution, subjects were presented with a visual stimulus giving information about the accuracy of their response. The stimulus providing feedback was named knowledge of results (KR). Specifically, the KR stimulus was a plus sign, a vertical line, or a horizontal line, which indicated that the response occurred late, early, of within the correct time window, respectively. EEG recordings obtained during the interval after the response execution and before the KR stimulus, showed a rising negativity prior to the onset of the expected stimulus, so-called stimulus preceding negativity (SPN). The increase in negativity prior to the onset of the KR stimulus was assumed to reflect the anticipation to the perception of the feedback sign. Therefore, the SPN elicited by the KR stimulus was an index of the perceptual aspect of PA. Brunia and Damen also found that there are two sources of the SPN, one in the prefrontal cortex and the other one in the parietal area, both areas known to be implicated in top-down attentional control (Fig. 7). In another study Chwilla and Brunia (1991a) presented to participants different feedback conditions, in which the KR stimulus provided true, false, or no feedback. The SPN was only found preceding true feedback, it was largely reduced when the information was false, and it was absent when the signal was omitted. This supports the notion that the SPN is associated with the processing of an upcoming stimulus event that is

relevant for subjects' behavior. Authors suggested that the KR stimulus that delivers relevant information has a motivational effect that may enhance the SPN.

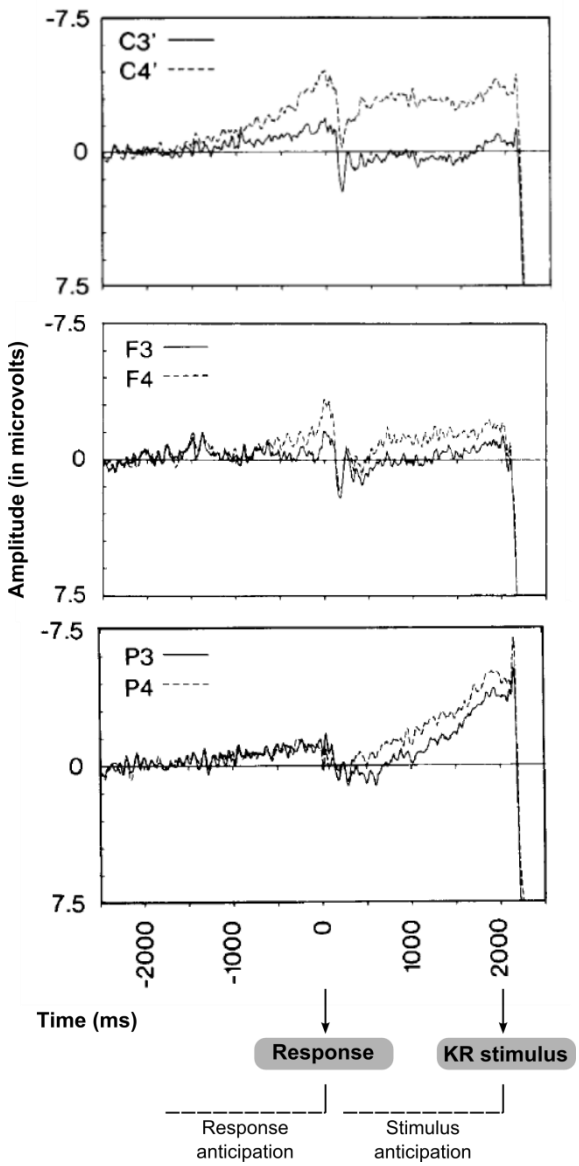

Figure 7. Stimulus Preceding Negativity recorded prior to a Knowledge of Results (KR) stimulus. The KR stimulus was presented 2000 ms after the execution of a response (adapted from Brunia & Damen, 1988).

The SPN was not only recorded before the presentation of the KR stimulus. When a stimulus giving an instruction is presented at a known moment in time, it is also preceded by a small SPN (Damen & Brunia, 1994). Also, a probe stimulus used to indicate a match with an earlier result is preceded by an SPN (Chwilla & Brunia, 1991b). These studies showed that the brain activity in different anterior and posterior areas is modulated when subjects are waiting for a relevant stimulus under various circumstances.

The activation of brain areas in preparation to the upcoming information processing cannot be sustained over long periods of time, especially when high levels of attention are required. Consistent with this aspect of PA, it was shown that voluntary PA is marked by relatively rapid fluctuations (Padilla et al., 2006). In an ERP study, Padilla et al. showed that the amplitude decrease in frontal CNV activity prior to the stimulus appearance was accompanied by a decrease in sustained negativity in extrastriate sites to the target stimulus. More importantly, this preparatory activity decrement was linked to the commission of errors in the behavioral task. This finding is consistent with the proposal that an increase in PA activity increases the probability to respond efficiently to the target.

Non-invasive electrophysiological recordings methods have a high temporal resolution, allowing a precise measurement of the time course of attentional processes (Luck & Girelli, 1998). However, they have a poor spatial resolution, making more difficult the correlation of specific brain areas with a given attentional process.

2.1.4. *Neuroimaging techniques*

Positron emission tomography (PET) and *Functional magnetic resonance imaging (fMRI)* methods provide a non-invasive image of the brain while subjects are implicated in different cognitive tasks. Whereas PET measures cerebral blood flow, fMRI measures deoxygenation signals in the brain (for more details, see Corbetta, 1998; Haxby, Courtney, & Clark, 1998). These methods assume that metabolic changes in the brain are correlated with neuronal activity.

An increasing amount of neuroimaging research has shown that attentional control mechanisms are regulated by frontal brain areas (Barceló et al., 2000; LaBerge, 1995, 1997; Padilla et al., 2006). Different studies demonstrated that top-down preparatory operations in frontal brain regions can modulate the activity in posterior cortex (Coull, Frith, Frackowiak, & Grasby, 1996; Gazzaley et al., 2007; Hopfinger, Buonocore, & Mangun, 2000; Jonides et al., 1993; Kastner, Pinsk, De Weerd, Desimone, & Ungerleider, 1999; McCarthy et al., 1996).

When a certain attribute of a target is known in advance it can induce a preparatory state in anticipation of the upcoming target, which is the case in match-to-sample tasks (LaBerge, 1995, 1999). In these tasks, a first stimulus (sample) is presented to subjects and a second stimulus (probe) is presented after a delay (maintenance period). Subjects are

instructed to indicate whether the probe matches the sample or not. Corbetta, Miezin, Dobmeyer, Shulman, and Petersen (1991) showed that when a sample cued a specific attribute of a probe stimulus, brain areas corresponding to these attributes showed more activation than they do when no specific attribute is cued. This finding indicates that the sample induces a top-down preparatory activity in the particular areas specialize in the attribute bottom-up sensory processing (attribute perception).

As in the match-to-sample task, precuing a spatial location may activate structures involved in the function to be executed, in order to ameliorate the final performance (Brunia, 1999). Thus, in cueing tasks, the storage of cued location information in working memory may be accompanied by attention to that location throughout the period of time between the cue presentation and target appearance (Awh, Anllo-Vento, & Hillyard, 2000; Jha, 2002). Consistent with the idea that working memory systems are closely related with control attention mechanisms, it has been recently shown that a persistent activity in similar areas of the prefrontal cortex and the posterior parietal cortex during the maintenance of a working memory representation, and spatial attention tasks (Ikkai & Curtis, 2011).

In a fMRI study, Kastner et al. (1999) reported activation in visual cortical areas prior to the presentation of an expected stimulus array in a specific location. Interestingly, the increased activity in cortical regions involved in the perception of the relevant stimulus location was registered in the absence of visual stimulation and was retinotopically location-selective. This study shows the anticipatory influence of attention in specific sensory brain regions, triggered by the simple expectation of the onset of the visual stimulus.

These neuroimaging techniques have the advantage of measuring brain activity across the entire brain with a relatively high spatial resolution. However, knowing that a particular area is more active at a given moment does not reveal what exactly that area is doing or how well it is doing it. This particular problem with drawing explicit conclusions about cognitive functioning only from brain activation can be added to the disadvantage concerning the low temporal resolution of the method. Neuroimaging techniques have poor temporal resolution compared to methods that directly measure neural events, such as ERPs.

In summary, each of these methods in cognitive neuroscience has its own advantages and limitations. The selection of one particular method to study the cerebral bases of visual attention is intrinsically related with the kind of questions we can ask. The design of studies

using different methods allows a more complete examination of the neural bases of attentional processing. The combination of the findings obtained in different attentional tasks, using different techniques, might be critical for evidencing the implication of specific brain areas in attentive behavior.

2.2. Neural networks underlying visual attention

In the past years, the evolution of the techniques in neuroscience previously presented allowed the study of the cerebral bases of cognitive processes in different task situations. The increasing amount of research in the field of visual attention demonstrates that not a unique region in the brain is the anatomical substrate of this cognitive function. In contrast, different cortical and subcortical areas underlie attentional mechanisms, interconnected in a specific neural system. From this perspective, there are several models concerning the distribution of brain networks involved in attentional processing.

In an influential article, Posner and Petersen (1990; for a recent review, see Petersen & Posner, 2012) proposed that the attentional system in the brain is anatomically separated from sensory and motor networks that continue to perform operations when attention is directed elsewhere. The attentional system is formed by different anatomical areas that are interconnected (Fig. 8). This system is subdivided into three subsystems or networks that perform different functions: orienting, alerting, and executive control (Fan, McCandliss, Sommer, Raz, & Posner, 2002). In an fMRI study, Fan, McCandliss, Fossella, Flombaum, and Posner (2005), demonstrated the anatomical independence of the cortical and subcortical substrates of each attentional network. This finding was supported in the literature by other neuroimaging and patient studies (Raz & Buhle, 2006). The alerting network, necessary to maintain a vigilant or alert state, has been associated with activity in frontal and parietal regions, particularly in the right hemisphere. The orienting network, involved when selecting specific information among multiple sensory stimuli, has been related to the activity in different areas such as the pulvinar, superior colliculus, superior parietal lobe, temporoparietal junction, superior temporal lobe and frontal eye fields. Finally, the executive network, involved in the control of conflict and in detection, has been associated with activity in the frontal cortex, specifically in the anterior cingulate cortex (ACC).

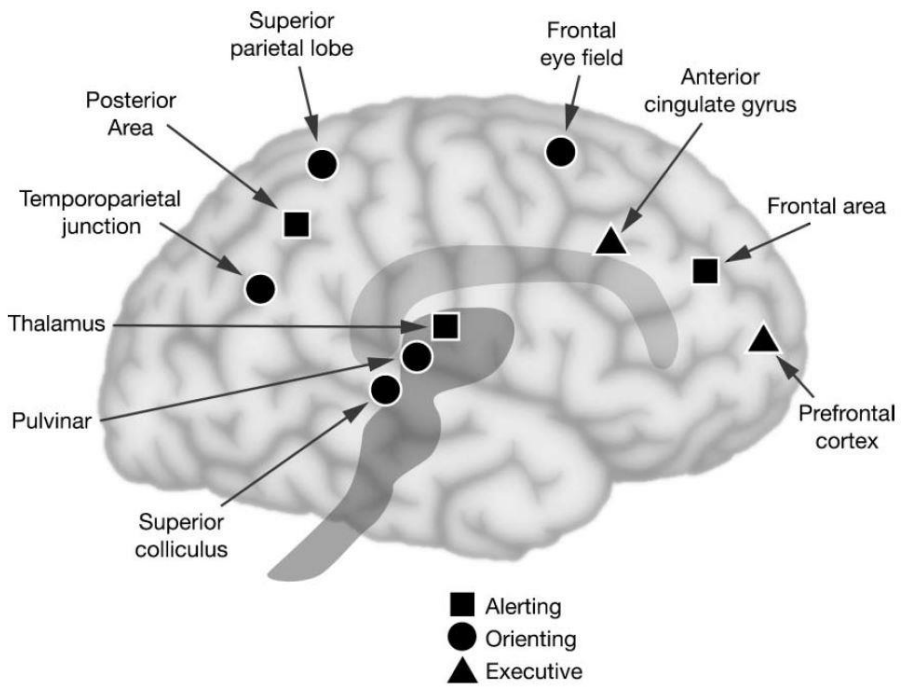

Figure 8. Anatomical areas of alerting, orienting, and executive attentional networks (from Posner & Rothbart, 2007).

Corbetta and Shulman (2002) proposed that two sets of brain regions in the dorsal and ventral frontoparietal cortex are recruited in selective attention. They separated the dorsal neural activity involved in goal-directed or endogenous attention network from the ventral network involved in the stimulus-driven or exogenous attention (Fig. 9) .The dorsal network is recruited during the voluntary allocation of attention elicited by a cue to a specific location or visual feature. This network has a sustained activity when attention is maintained over long periods of time, such as tens of seconds. The activity of the dorsal network can be interrupted by the appearance of an unexpected but behaviorally relevant event occurring at an unattended location, such as an invalidly cued target. In this situation, a ventral network is activated in order to orient attention to the novel stimulus. The relevance of these two networks in selective attention and their neural substrates have been recently supported by other studies (Sestieri, Shulman, & Corbetta, 2012). The dorsal network is the primary network recruited under all conditions in which selective attention is prepared and engaged and this network is supplemented by a second ventral network under conditions in which attention has to be reoriented from the actual focus to a behaviorally relevant stimulus.

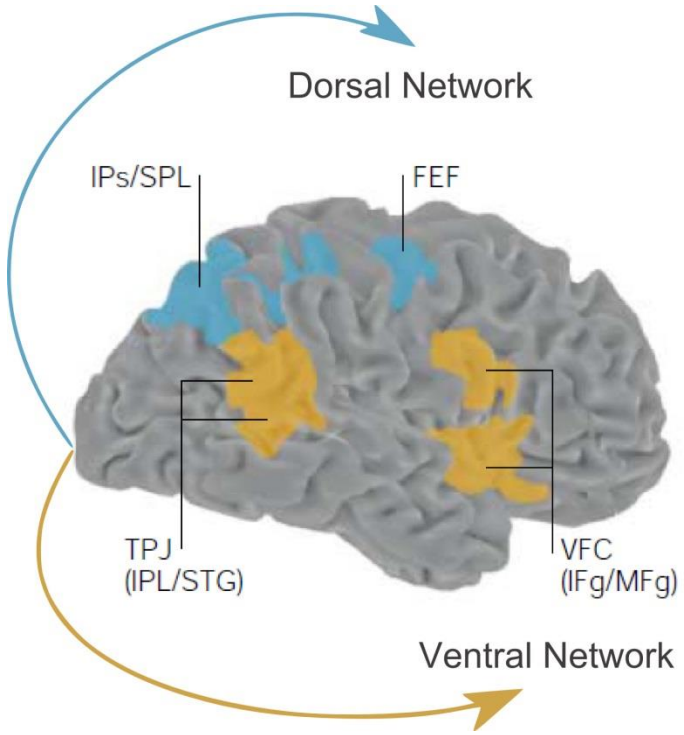

Figure 9. Dorsal and ventral frontoparietal networks colored in blue and orange, respectively (adapted from Corbetta & Shulman, 2002). *Abbreviations*: FEF, frontal eye fields; IPS, intraparietal sulcus; SPL, superior parietal lobule; TPJ, temporal–parietal junction; IPL, inferior parietal lobule; STG, superior temporal gyrus; VFC, ventral frontal cortex; IFg, inferior frontal gyrus; MFg, middle frontal gyrus.

LaBerge (1995, 1997, 2002, 2005) has proposed a different theory based on a cognitive-neuroscience approach in terms of the control, expression, and the mechanism of attention in brain pathways. The theory assumes that attention is an event in the brain that requires the simultaneous activity of three brain regions connected by a triangular circuit, corresponding to three components of attentional operations. These components are the expression of attention in a particular (selected) brain sensory pathway, localized in posterior cortical areas; the mechanism that enhance the level of activation relative to the degree of attentional concentration (filter), localized in the thalamus; and the control of the expression and mechanism, which is localized in the frontal cortex. The triangular circuit can be initially activated by two different classes of sources: internal (within the system), and external (outside the system). However, the activation of cortical sites of attentional expression by external sources is considered an attentional event only if this brief and rapidly decaying activation is sufficiently enhanced and sustained through the cortico-thalamical pathway. Thus, according to these assumptions an attentional event is essentially endogenous. As the

present thesis is framed in these theoretical assumptions, the triangular theory of attention is described with more detail in the next section.

2.3. The theory of LaBerge

2.3.1. *The triangular circuit theory of attention*

The triangular circuit theory assumes that attentional operations increase the signal-to-noise ratio, in order to emphasize the target processing relative to distractor processing (LaBerge, 1995, 1997). The *expression* of attention is defined as the enhancement of activity at the target site relative to the activity at the distractor site. This enhancement is assumed to take place in posterior cortical areas in which target and distractor signals are represented. The regions of attentional expression are distinguished from the circuit mechanisms that produce this activity differences.

The *mechanism* of attention is mediated by the thalamus that operates by coding the target and distractors locations and providing the interactions between these locations codes. The thalamus acts as a filter and as an amplifier of attentional expression. Particularly, the pulvinar nucleus of the thalamus has a special role in filtering information when the target is more difficult to distinguish from distractors (e.g. in situation in which target and distractors are proximal), and in enhancing the selected information (LaBerge & Buchsbaum, 1990). When stimuli are clustered together, there is a higher amplification of the pulvinar to achieve stimuli resolution, compared to a condition in which target and distractor are well separated. Therefore, the amount of the pulvinar amplification is related to the attentional demands of the task, which increases, for example, as the spatial distance between target and distractor stimuli becomes smaller.

The *control* aspect of attention regulates the attentional activity directed to a target and distractor event. The amount of activity would depend on the expectation for those events stored in working memory. This expectation might be modulated by an instruction and/or by the stimuli probability. The triangular circuit theory assumes that the attentional control in frontal brain regions is subdivided into two pathways: the brief or *selective* pathway and the prolonged or *modulatory* pathway, both serving different aspects of attention (Fig. 10).

The selective control pathway is assumed to operate quickly (in milliseconds) because brain cortical columns are presumed to function at low intensities and therefore take less time to reach effective levels. Selective attention works at low attentional intensities and is represented by low attentional activity in brain sites of attentional expressions, allowing more shifts of attention per unit of time. This rapid operation is useful as it can be produced quickly after attentional shifts to a new location or new objects, like in tasks of searching for a target in a crowded environment. The selective control has a crucial role in determining *where* and to *what* attention is directed. In addition, selection is assumed to influence the duration of attention, that is, *how long* a particular cortical area will be activated. On the other hand, the modulatory control pathway is assumed to operate relatively slowly (in seconds) because cortical columns must take time to develop moderate to high intensities (LaBerge et al., 2000). Longer durations necessary to the production of high attentional intensity are more typically found in preparation tasks where the target is displayed very briefly following a long preparatory interval (LaBerge & Buchsbaum, 1990; LaBerge et al., 2000; LaBerge & Brown, 1989) or by using an appropriate motivational instruction (LaBerge et al., 2000, Experiment 2). Thus, the modulatory control has a crucial role in determining *how intense* the activity will be in cortical sites of attentional expression that represent the selected signal (LaBerge et al., 2000).

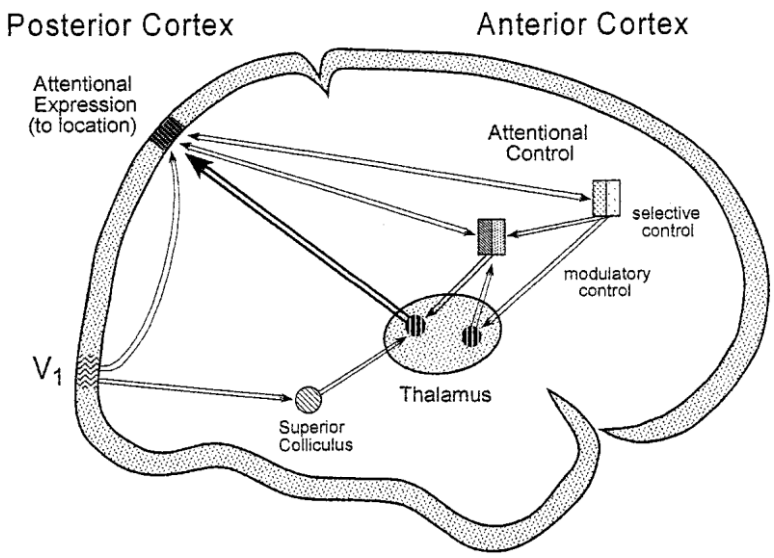

Figure 10: Selective and modulatory control modules in the triangular-circuit theory of visual attention to a spatial location (from LaBerge, Auclair, & Siéroff, 2000).

The selective and modulatory types of attentional control are consistent with studies describing the characteristics of the electrical activity within the cortical neurons. It has been proposed that within the thalamocortical circuit, the sustaining of attention during the preparatory period is expressed by oscillatory waves in apical dendrites of pyramidal neurons and brief attention takes the form of pulse processing in the short basal dendrites (LaBerge, 2005). This theoretical proposal is related to the sustained cortical activity registered with EEG as a persistent negativity in frontal and parietal areas during periods of anticipating a stimulus (Barceló et al., 2000; Brunia & Damen, 1988; Brunia, 1999; Padilla et al., 2006).

2.3.2. *Modulation of PA toward a spatial location*

The triangular circuit theory of attention distinguishes the simple brief selection of a target location, from the selection and enhancement (modulation) of preparatory attentional activity of the selected location. The preparatory attentional activity directed to a particular target location corresponds to the prolonged attentional manifestation in brain regions that codes a particular location prior to the appearance of an expected event in that location. The pre-activation of the posterior cortical maps corresponding to this location is controlled by frontal cortical regions that not only select the relevant spatial location but modulates the corresponding intensity of activation. During periods of prolonged PA to an object's location, activity may persist in frontal areas of attentional control and in parietal areas of attentional expression. Persistent activity in attentional expression influences the early processing of the location information arising from an upcoming target stimulus, modulating in turn information coming from sensory pathways.

In a condition where a target and/or distractor are expected, the selective control module registers the effects of the instruction indicating which location has to be selectively attended, as well as recent target and distractor events. To produce PA by the modulation of expectancies, the selective control must activate corresponding target and distractor sites in the modulatory control module. In turn, the modulatory control activates the target and distractor sites in posterior cortex, intensifying the activity in one or the other site relative to expectations. When the target signal occurs, this signal will be potentiated by the activation produced by the modulatory control. In this way, attention modulates the processing of incoming sensory information.

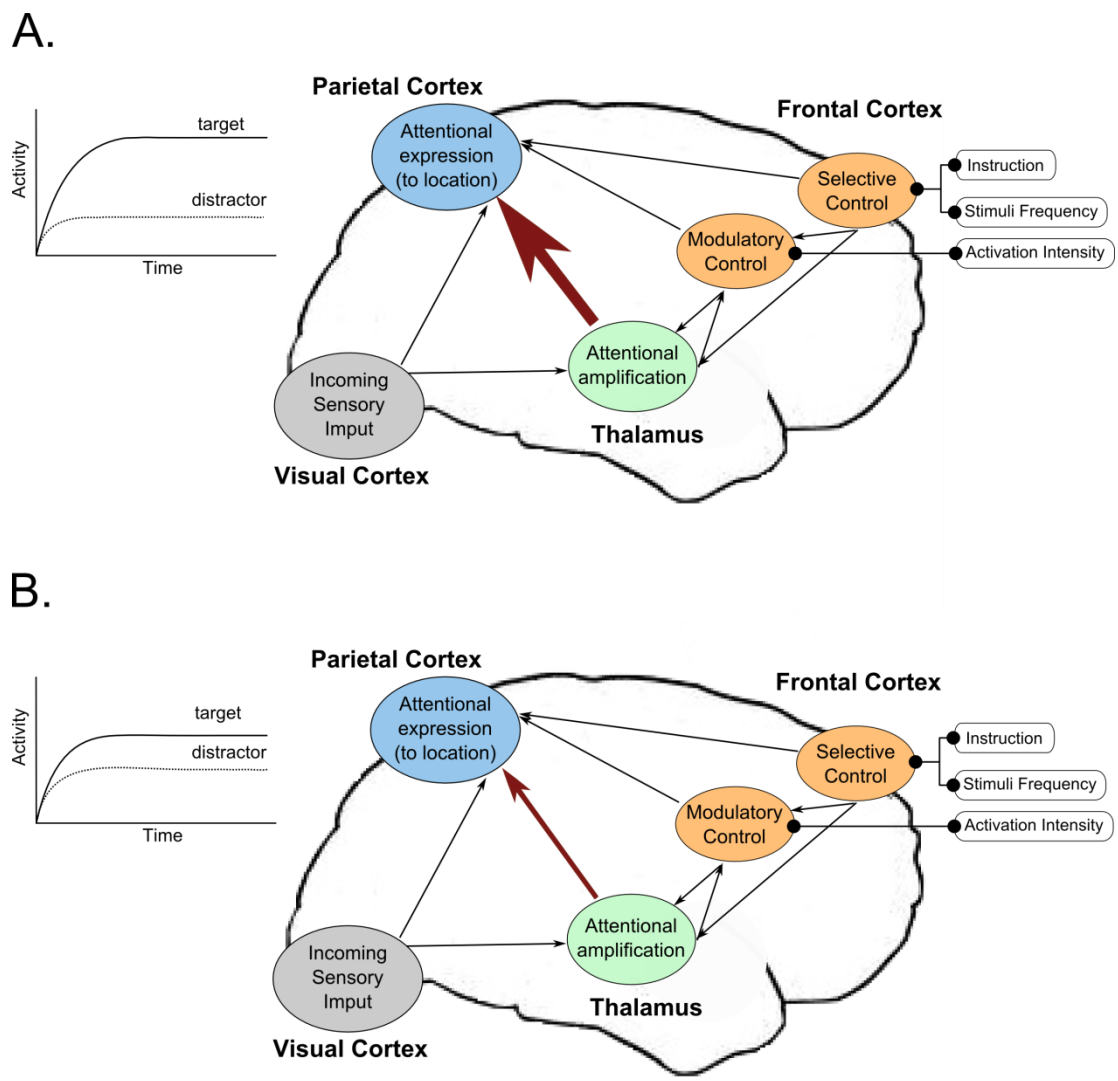

Figure 11. Illustration of the target site modulation by the thalamocortical circuit as a function of distractors probability. A. In a condition with low distractor probability, the preparatory attentional activity directed to the target location is enhanced (thick red arrow), reaching high intensities. B. In a condition with higher distractor probability, the attentional activity directed to the target location decreases (thin red arrow), maintaining its activity to low levels.

The accumulated records of recent target and distractor occurrence in control areas produce attentional activation of both targets and distractors sites as a function of their frequency in the past. As a consequence, there is an attentional bias toward potential targets and distractors before the presentation of the target display. The attentional activity generated during the target display is added to this bias to determine the speed of processing of the target stimulus. If targets and distractors have different probabilities of occurrence, the probability distribution is assumed to influence the intensity of PA directed to one or the other location. When targets are more probable than distractors, the intensity of PA directed to the site of attentional expression corresponding to the target location is higher than to the intensity of PA directed to the site corresponding to the distractor. The attentional bias

towards the target location (Fig. 11A) corresponds to faster processing in that location. In contrast, when distractors are more probable to occur, PA to the target site will have lower levels of activity. Less attentional bias towards the target location (Fig. 11B) corresponds to slower processing in that location.

2.3.3. *The attentional preparation test: a paradigm to measure the modulatory control of PA.*

LaBerge et al. (2000) developed a simple paradigm, referred as *Attentional Preparation Test* (APT), in which they attempted to experimentally separate the selective (brief) and modulatory (prolonged) control of attention, both serving preparation. The APT measures the ability of subjects to modulate the intensity of PA directed to a target location as the probability of a distractor appearing in a near location increased. The logic of the APT is to vary the amount of PA directed to a target location by occasionally presenting distractors during the time interval prior to the target occurrence. If a distracting stimulus appears when a subject expects a target stimulus, it might compete for the allocation of PA. Increasing the probability of the distracting stimulus might also increase its competitive strength. When the probability of the distracting stimulus is high, relatively less PA should be allocated to the target, increasing RTs.

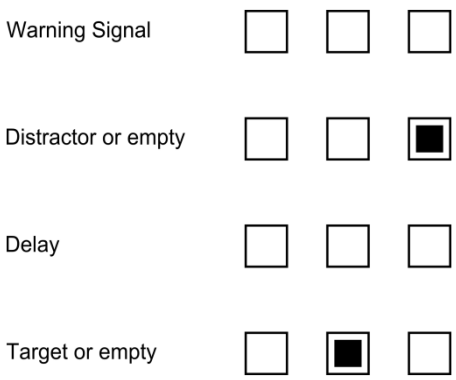

Figure 12. Example of a sequence of stimuli presented on a trial in the Attentional Preparatory Test (adapted from LaBerge et al., 2000).

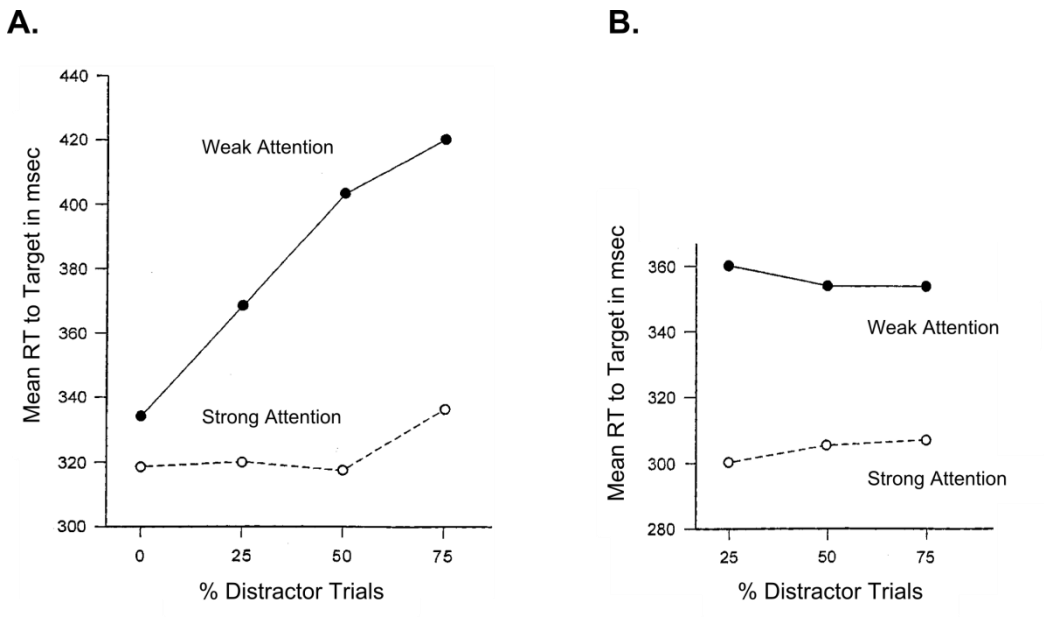

Figure 13. Mean response times to the target as a function of distractor-trial percentage for weak and strong instruction conditions. A. Data from trials in which the distractor did not appear but was expected to occur. B. Data from trials in which a distractor preceded the target presentation (see text for details). From LaBerge et al., (2000).

In the APT, three empty boxes were presented horizontally on the screen at the beginning of each trial, this event acting as a warning signal (see Fig. 12). The target consisted in a black square in the central box and it could appear after a variable delay of approximately 2 seconds. A distractor, a black square in one of the lateral boxes, could appear at the time interval between the warning signal and the target onset, at a delay of approximately 1 second. Thus, the distractor occurred in the preparatory phase preceding the occurrence of the target. In order to minimize selective attention effects, the target never appeared simultaneously with the distractor, and the three boxes were sufficiently separated to reduce errors to a negligible level. Long delays were chosen because PA takes time to develop (for a review, see Jennings & van der Molen, 2005). Participants were instructed to respond when the dot appeared in the central location and to not respond when it appeared in one of the two lateral boxes, so-called “weak” instruction condition. The frequency of trials containing a distractor varied in several blocks with 0%, 25%, 50%, and 75%, respectively. In the APT, there were two types of trials containing a target: trials in which the target was preceded by a distractor and trials in which only a target occurred. Whereas in the first type of trials the distractor may function as a cue (or a reinforced warning signal) that the target is

about to appear, in the second type of trials the distractor is assumed to act as a competitor for PA. It was hypothesized that an increase of the frequency of trials containing a distractor should be accompanied by a relative decrease of the amount of PA directed to the target location from the beginning of the trial. As a consequence, slower RTs to targets should be obtained as a function of distractor probability in trials in which it competes for PA to the target, i.e. in trials in which only a target occurred.

The results of this experiment showed a different pattern of responses for targets appearing alone within a trial and for targets preceded by a distractor. For trials in which the distractor did not appear but was simply expected to occur there was a linear increase in the RTs as a function of the probability of distractors (Fig. 13A, Weak Attention slope). In these trials, subjects presumably form expectations for distracting stimuli, especially in the block where they often occur before target onset (75%). Thus, frequent distractors may compete with PA to an upcoming target, causing for less PA to be allocated to the target. This finding suggests that the observers' PA for the occurrence of targets as well as distractors was regulated by their appearance in recent trials. However, once a distractor occurred, there was no expectation concerning a distractor, because distractors occurred only once in a trial. Indeed, the RTs in trials containing a target following a distractor were not modulated by distractor probability (Fig. 13B).

LaBerge et al. (2000) also demonstrated that the amount of PA directed to the target and distractors could be regulated by the motivational properties of an instruction. They showed that instructing participants to attend "only to the central box" (rather than simply respond to the target) created a "basal-ganglia" motivational state in which only the central box is "of interest" for the subject. In this condition, called "strong" instruction condition, participants were assumed to enhance the preparatory attentional activity directed to the target location. This enhancement results in an increase of the signal-to-noise ratio, and, thus, in a reduction of the effects of recent distractor presentation. In this condition, they found a near-zero slope for targets appearing alone within a trial (Fig. 13A, Strong Attention slope).

The series of studies carried out by LaBerge et al. (2000) shows that it is possible to modulate the intensity of PA directed to a target location, by changing the relative frequency of targets and distractors in a block of trials, or by an appropriate instruction. Because the selection involvement is rather low (simple detection task, and no simultaneous distractor with the target), this paradigm provided the possibility to evaluate the effects of modulatory control of attention more or less independently of the selective control of attention.

2.3.4. *The APT and the frontal cortex modulation of PA*

The ability to enhance PA to a target location is assumed to be located in frontal areas (LaBerge et al., 2000). A neural damage in the frontal cortex should affect the modulation of PA and the capacity to inhibit the interference from distractors. The role of frontal regions in attentional modulatory control was addressed in two studies with frontal damage patients. In one study the APT was given to adults with the frontal form of fronto-temporal dementia (Siéroff et al., 2004), and in the other study the test was administrated to children with frontal or temporal lobe epilepsy (Auclair, Jambaqué, Dulac, LaBerge, & Siéroff, 2005). In both studies, frontal patients showed larger effects of the probability of a distractor appearance than normal controls, taking longer to respond to the target (Fig. 14). These results show that the ability of resisting the effects of distractors in the preparatory period before the target presentation is impaired in frontal patients. These patients certainly present a deficit in enhancing attention toward the target location during extended delays. The findings obtained in patients with frontal damage suggest that the APT might be a sensitive test to measure the ability of the frontal cortex in modulating PA towards a spatial location.

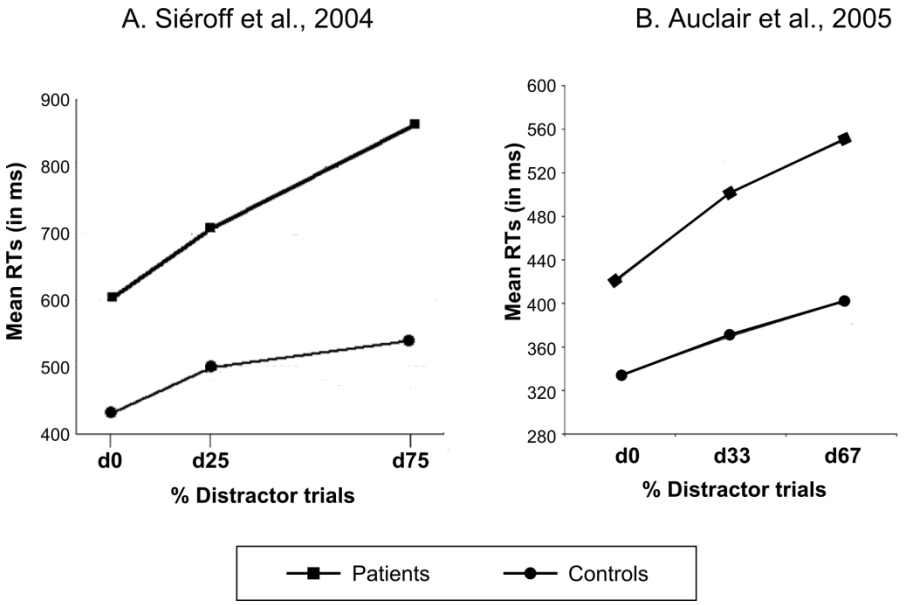

Figure 14. Reaction-time results of two studies using the APT in patients with frontal damage. Compared to control subjects, the ability of modulating PA to the target location was impaired in frontal patients. A. Experimental study in adult patients with frontal lobe lesions (from Siéroff et al., 2004). B. Experimental study in children with frontal epilepsy (from Auclair et al., 2005).

2.4. Conclusion

The triangular circuit theory of attention is used to frame the study of preparatory attentional processes in the present thesis. This theory distinguishes three components of attentional operations located in three different brain regions connected by a triangular circuit: the expression of attention in posterior cortical areas, the mechanism of attention in the thalamus, and the control of attention in the frontal cortex. The expression of PA in these pathways corresponds to the enhancement of the information flow from a selected target stimulus. However, PA directed to a target prior to its onset is not considered as an all-or-none operation, but is assumed to be a continuously variable modulatory process (LaBerge, 1995). The modulatory control of attention is a prolonged aspect of attention, and regulates the intensity of brain activity directed to regions of attentional expression. The selective control of attention is a brief aspect of attention, and determines the regions (cortical columns) of attentional expression. The selective and modulatory aspects of attention are subtended by different neural mechanisms and intervene in different situations. According to LaBerge (1995), selection has a specific role in attention because it determines the stimulus on which attention will focus, and the modulation enhances the representation of this stimulus so that it can reach the level of consciousness (mindfulness); attention per se combines these two aspects. LaBerge et al. (2000) proposed a simple paradigm to measure the modulatory control of PA directed to a spatial location, the APT. Studies using this experimental paradigm demonstrated that the intensity of PA directed to a spatial location can be modulated by the probability of the occurrence of an expected stimulus in that location. Brain lesion in the frontal cortex damaged this modulatory capacity. Thus, the APT might be considered as a reliable and simple method to measure the brain capacity of modulating attentional activity directed to a spatial location prior to the occurrence of an expected target event.

CHAPTER 3: Preparatory attention and brain hemispheric differences

3.1. Brain hemispheres and visual information

One of the mysterious aspects of the human brain is the nature of its division into two halves: the LH and the RH. Most sensory information arising from each half of the body or space typically projects only directly, or preferentially to the contralateral cerebral hemisphere. Specifically in vision, neurons of the temporal half of each retina project to the visual cortex of the ipsilateral hemisphere, and neurons of the nasal half of each retina projects to the visual cortex of the contralateral hemisphere. As a consequence, when eyes are fixated to a point in space, the information arising from each side of fixation or visual field projects directly to the contralateral visual cortex (Fig. 15). This contralateral projection might be true even in the foveal area (Lavidor & Walsh, 2004).

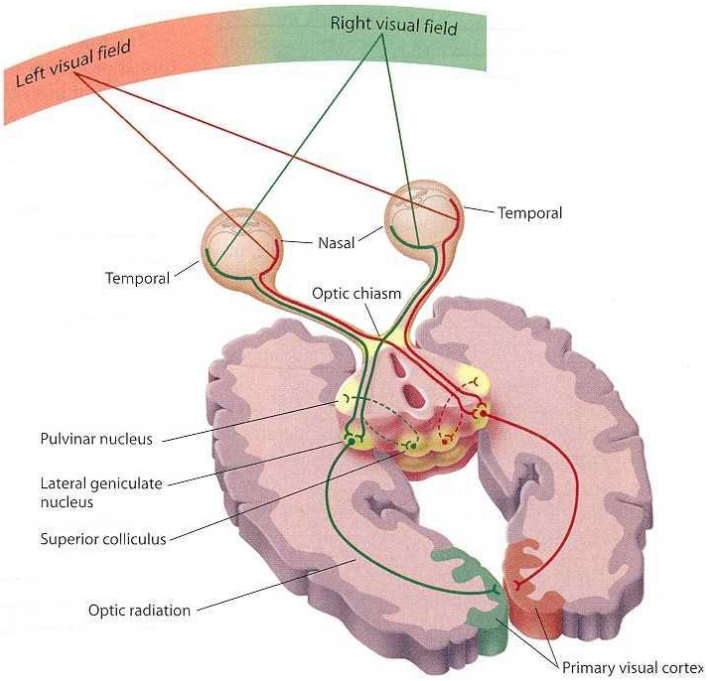

Figure 15: Schematic anatomical arrangement of the human visual system. Information arising from each visual field is projected to the visual cortex of the contralateral brain hemisphere (from Gazzaniga, Ivry, & Mangun, 2009).

The results of an increasing amount of studies interested in functional lateralization suggest that most cognitive functions are differentially lateralized. The proposal of hemispheric specialization in language, memory or attention has traditionally relied on different methodological approaches. The hemispheric specialization also affects perception, and it has been shown that the two sides of the human brain are not symmetrical in visual information processing. In the next section, we will present the different methods to explore functional brain asymmetry. In the following sections, we will present some of the conclusions from these different methods on the differential hemispheric involvement in attention, and more precisely in PA.

3.2. Different methods to study brain hemispheric differences in visual attention

3.2.1. *Neuropsychological method: studies on patients*

A widely used method to study functional asymmetries in the cortical hemispheres, and historically the first one, is the brain lesion method. Unilateral lesions allow the investigation of the correlation of a focal brain area with a particular cognitive function. The brain lesion approach has been broadly developed to study hemispheric differences after the work of Paul Broca, which demonstrated that injuries to homologous areas of the two hemispheres do not have similar effects in cognition. He showed that lesions of the inferior frontal lobe in the LH but not in the RH damaged the cognitive ability of language articulation (Broca, 1865). Since this finding, several investigations have discovered the impairments of other higher mental functions following unilateral cerebral damage. The advantage of studies using this approach is that, given that the damage is lateralized in the brain, any impairment in the processing of stimulus information can be linked to the damaged region, even if the stimulus is presented at fixation.

Another opportunity to study lateralization of cognitive functions is to investigate the performance of patients, known as *split-brain* patients, suffering from irremediable epilepsy. In these patients, the fiber tract connecting both hemispheres (*corpus callosum*) has been surgically split, resulting in a disconnection of the hemispheres. As these fibers are crucial to exchange information between hemispheres, the research in split-brain patients has opened a

unique opportunity to study the independence of hemispheric functioning (see Gazzaniga, 2000). It is necessary to isolate the stimulus presentation and the response execution to only one hemisphere in order to examine the competence of a single hemisphere in a visual attention task. The *divided visual-field paradigm* consists in presenting a visual stimulus very briefly to the LVF or the RVF, when the eyes of individuals are fixated appropriately in the center of the screen. The duration of the stimulus must be brief enough to prevent eye movements directed to the stimulus and provoking fovealisation. As a consequence, only the hemisphere contralateral to the stimulated visual field receives the stimulus on each trial. Studies in split-brain patients using the divided visual-field paradigm give the possibility to examine whether the two hemispheres have equivalent abilities in visual attention tasks. Nevertheless, as it was stated in Chapter 2, although studies in patients have advantages, they also have some limitations. For example, it might be difficult to generalize conclusions from split-brain patients to neurologically normal individuals, because the callosal surgery is done on a damaged brain (Whitaker & Ojemann, 1977). It is thus important to examine hemispheric differences in neurologically intact individuals in order to have a detailed knowledge of the hemispheric asymmetry in human cognition.

3.2.2. *Measuring and modulating localized brain activity in neurologically intact individuals*

In Chapter 2, many different methods allowing for the analyses of the brain activity during attentional demanding tasks were presented. The relatively recent development of these techniques in neuroscience allows *in vivo* studies of both structural and functional asymmetries. The involvement of such techniques to study brain asymmetries extended the possibility of neuropsychological approaches.

The underlying assumption of methods measuring electrophysiological and/or metabolic brain activity is that a certain area of the brain will be more active if it is particularly involved in the information processing of a given task. In the frame of hemispheric differences research, studies aim to determine whether some tasks involve more activation from an area within one hemisphere than from the homologous area within the other hemisphere. Some of these methods were shown to have good spatial resolution (PET, fMRI), while others have good temporal resolution (ERPs). However, there are certain

limitations to extract conclusions about hemispheric cognitive processing only from the activation of a certain region. Furthermore, each of these methods has specific constraints that were briefly presented in Chapter 2.

Another possibility to study hemispheric differences in a specific cognitive function is to modulate the normal brain activity. Techniques like TMS and tDCS create “virtual lesions” in the normal brain, allowing the examination of the extent to which a stimulated region in one hemisphere and not its homologous area in the other hemisphere is involved in the performance of a given task. Although these methods of brain stimulation present an interesting opportunity to study lateralization of certain cognitive functions, they present several constraints and can cause undesirable side effects when used in normal population (see Chapter 2).

3.2.3. *Behavioral assessment in neurologically intact individuals*

Another group of methods to study functional asymmetries in the brain corresponds to the behavioral assessment of hemispheric performance of neurologically intact individuals. In this population it is not possible to test the competence of one hemisphere in isolation (like in split brain patients), as they have the full potential of hemispheric interaction. However, it is possible to examine the speed and accuracy with which humans performed a task, as a function of which hemispheres directly receive the stimulus and initiate processing. Based on the anatomical crossing of sensory visual pathways (Fig.15), the divided visual-field paradigm is a widely used technique to study hemispheric processing of visual information in healthy individuals. Any difference in performance is assumed to reflect differences in hemispheric functioning (Kimura, 1966, 1969), and may be associated with differences in hemispheric control of the visual space (Corballis & Gratton, 2003).

Recently, a few studies examined the validity of behavioral laterality measures by comparing them with brain imaging data. For example, Van der Haegen, Cai, Seurinck, and Brysbaert (2011) investigated the validity of behavioral measures to study hemispheric dominance in language processing. The results of behavioral language tasks (word and picture naming tasks) using the divided visual field paradigm were compared with the brain activity measured while subjects performed a word generation task in fMRI. They reported that visual field dominance in behavioral measurements correlated with lateral brain activity measured

with fMRI. This result suggests that the behavioral tasks using the divided visual field paradigm may provide useful information about the direction of hemispheric dominance for a given cognitive ability. Thus, the divided visual-field technique might be considered as an efficient technique to study hemispheric specialization in healthy participants.

The behavioral assessment in neurologically intact individuals using the divided visual field paradigm presents several advantages when compared to the other methods. The behavioral study of healthy individuals allows more reliable interpretations about normal brain functioning compared to studies in patients. In addition, the behavioral assessment approach is less time-consuming and does not require very expensive apparatus, or very specific analyses of output signals compared to electrophysiological or imaging techniques, making it more accessible to all experimental researchers. Finally, the method gives behavioral conclusions that might have an information value independent of the brain hemisphere hypotheses: it is behaviorally relevant to know that we may not process information in the same way, and with the same efficiency in different parts of the visual field. Thus, the divided visual-field method might be considered as a reliable, less-expensive and easy way of examining lateralization. The method has also its own limitations, like every method, mainly that the conclusions on the functional hemisphere specialization are indirect, and do not give a precise location map of the hemispheric specialization.

3.3. Hemispheric differences in visual attention

There has been a long debate about the role of each hemisphere in attentional processes. Some researchers suggested that the right hemisphere is dominant for spatial attention (Heilman & Valenstein, 1979), and the left hemisphere is dominant in the control of attention (Posner & Petersen, 1990). Others suggested that each hemisphere plays a specialized role in the attentional modulation of visual perception (Reuter-Lorenz, Kinsbourne, & Moscovitch, 1990). Kinsbourne (1970) has proposed a theory of hemispheric differences in the control of spatial attention that relates activation hemispheric asymmetries with the lateral control of attention in the visual field. The basic assumption states that when engaged in a specific task, the dominant hemisphere for this specific task takes the control of attention and behavior. When one hemisphere's activation is asymmetrically increased, it can elicit an attentional bias in favor of the contralateral visual field. In other words, when one

hemisphere is engaged in a specific task, spatial attention is directed towards the contralateral visual field, producing an advantage in performance.

In spatial attention, several studies suggest that the RH and the LH in humans make differential contributions to the selection of visual stimuli (see Siéroff & Auclair, 2002). The specificity in the contribution of each hemisphere has been examined in different task sets and a variety of dichotomies have been proposed in attentional processing of visual information. We will present three of them.

3.3.1. *Location based vs object based visual attention*

Visual attention can be primarily allocated to either where an object is located in space (space-based attention), or to the structure of the object (object-based attention). In has been suggested that the RH visual attention is location-based while the LH visual attention is object-based (Arrington, Carr, Mayer, & Rao, 2000; Egly, Driver, & Rafal, 1994). Egly et al. (1994) proposed a clever procedure based on the cuing paradigm to show both location-based and object-based components in visual selection (Fig. 16). Subjects were shown two rectangles that appeared either above and below fixation (horizontally displayed) or to the left and right of fixation (vertically displayed). The cue consisted in the brightening of one of the extremity of the rectangle, which was followed by a target (a solid square in one of the extremity of one of the rectangles). Participants had to make a simple response to the onset of the target. The cues were either valid (cue and target at the same extremity) or invalid (cue and target at different extremity). There were two types of invalid trials: one in which the target was in the same rectangle as the cue (invalid same object) and the other in which the target appeared in the uncued rectangle (invalid different object). The distance between the cue and the target was the same in these two different invalid conditions. The latter invalid trial type was associated to a non-spatial component of orienting (object-based selection).

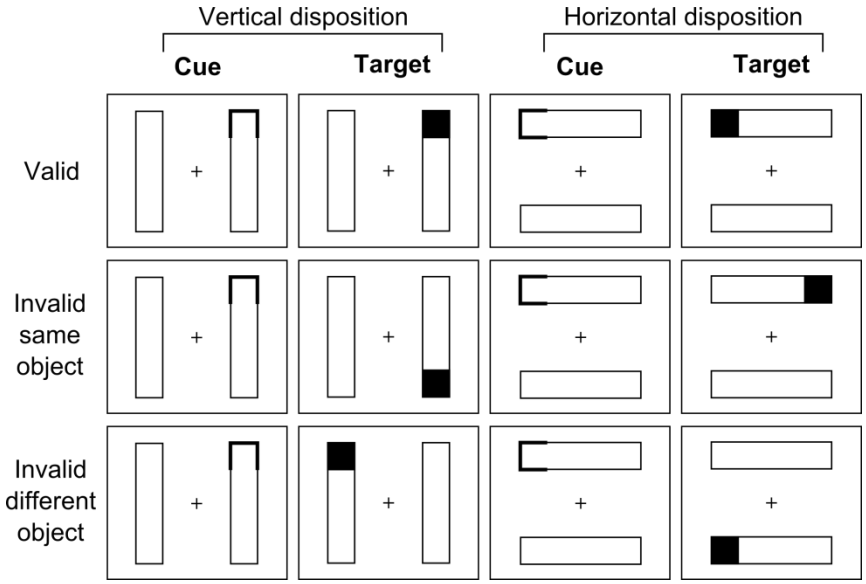

Figure 16: Sample displays from Egly, Driver, and Rafal (1994). See text for details.

Egly et al. (1994) reported that location-based and object-based forms of attentional selection were dissociable in brain-damage subjects. Patients with damage to the right parietal lobe showed a deficit in moving attention between spatial locations in the contralesional visual field relative to the ipsilesional visual field, whatever the type of invalid condition, whereas patients with damage to the left parietal lobe showed a deficit in moving attention between objects in the contralesional visual field, that is in the invalid different object condition. In a split-brain patient study, Egly, Rafal, Driver, and Starrveveld (1994), came to the same conclusion. Whereas attentional selection in the disconnected RH was preferentially location-based, attentional selection in the disconnected LH was object-based. Consistent with these studies showing hemispheric differences in visual attention towards objects and locations, the research in working memory demonstrated that object and spatial working memory are mediated by different systems, lateralized to the LH and RH, respectively (Smith et al., 1995).

3.3.2. *Spatial attention: processing coordinate vs categorical spatial relations*

In the literature, there is a general agreement that the RH is superior to the LH in processing visuospatial information (Vogel, Bowers, & Vogel, 2003). As it was described in

the previous section, the RH may be more efficient in directing attention to spatial locations. However, other studies claim that the hemispheric specialization in spatial processing depends on the kind of spatial representation used to accomplish a certain task. Given that the processing of visual information depends on the spatial relations established between elements present in the visual display, Kosslyn and colleagues (Kosslyn, 1987; Kosslyn et al., 1989) proposed that the brain computes two different kinds of spatial relations representations. One type of representation, named as categorical, is used to assign a spatial relation to a category, such us “above”, “below”, “in the middle”. The other type of representation, named as coordinate, is used to represent precise distances and locations in a metric coordinate system (object A and object B are about 2 cm apart). Authors also argued that there is a hemispheric dominance in the development of each type of representation. In a divided visual-field study, Kosslyn (1987) reported that categorical relations are computed faster when stimuli are projected to the RVF/ LH and coordinate relations are computed faster when stimuli are projected to the LVF/RH. After this finding came into light, several studies tested Kosslyn’s hypothesis of hemispheric asymmetry in computing these kinds of spatial relations (Michimata, 1997; Slotnick & Moo, 2006; Trojano et al., 2002, 2002; van Asselen, Kessels, Kappelle, & Postma, 2008; Van der Lubbe, Schölvinck, Kenemans, & Postma, 2006). Even though there are individual variations in strength and directionality of complementary lateralization, there is a large amount of regularity. In general, researchers suggest that the RH makes a more effective use of coordinate or metric distance relationships, whereas there is either no hemispheric asymmetry or a LH advantage for processing categorical spatial relationships (Jager & Postma, 2003).

3.3.3. *Global vs local processing of visual information*

In the visual space, individuals can focus their attention on a narrow area or they can spread it over a wider area (Eriksen & Yeh, 1985). The study of the distribution of attention towards the global information of a visual scene or the local details has been traditionally examined using hierarchical stimuli. A hierarchical stimulus consists in a global shape formed by smaller (local) shapes. Navon (1977) proposed an interesting paradigm to measure global and local processing of the stimulus display: he presented large letters made of smaller ones and asked participants to respond to the target letter that could appear in the global (large letter) or the local (small letters) level (Fig. 17). Using this paradigm, studies on participants

with unilateral brain damage (Delis, Robertson, & Efron, 1986; Lamb, Robertson, & Knight, 1990) and divided visual-field studies in neurologically intact individuals (Van Kleeck, 1989) claimed that there might be a hemispheric specialization for the attentional processing of global and local visual information. The RH was shown to be superior to the LH for allocating attention to wider areas of the visual field, whereas the LH was superior to the RH for concentrating attention to smaller areas of the visual field. Functional hemispheric lateralization in directing attention to wide or narrow areas of space has been also investigated with brain imagery (Heinze, Hinrichs, Scholz, Burchert, & Mangun, 1998; Lux et al., 2004), arriving to similar conclusions: a RH superiority for the processing of global levels of visual information and a LH superiority for the processing of local levels.

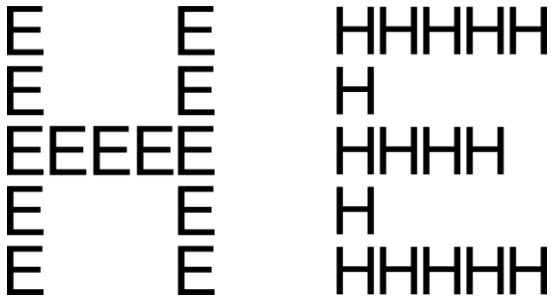

Figure 17: Examples of hierarchical visual patterns composed of small letters (the local level) arranged in the shape of a large letter (the global level). In the first example (left of the figure) the letter E is in the local level and the letter H in the global level. The second example depicts the opposite pattern (right of the figure).

The hemispheric dichotomies briefly presented here were centered on the level of representation to be attended (object-based, location-based), the type of spatial relations between elements in space (categorical, coordinate), and the size of the relevant information in the stimulus display (global, local). These dichotomies can be related to the attentional operations involved in the selection of a relevant target stimulus. According to LaBerge's theory (1995, 1997, 2002), the simple selection manifestation of attention can be distinguished from the preparatory manifestation of attention. In preparation there is a modulation (enhancement) of attentional activity prior to an expected target occurrence. This raises the question of whether there is hemispheric specialization in the modulation of the intensity of PA directed to an expected event.

3.4. Hemispheric differences in PA: the modulatory control across hemispheres

The intensity of PA activity directed to the target location is assumed to be a modulatory process that depends on the neural activations of different cortical and subcortical areas. The role of different brain regions in PA has been investigated in the past years under different tasks and context situations (Brunia & Damen, 1988; Corbetta et al., 2005; Luks, Simpson, Dale, & Hough, 2007; Small et al., 2003; Stern, Wager, Egner, Hirsch, & Mangels, 2007). However, it is not yet clear whether there is a hemispheric specialization in the preparatory aspects of attentional control (Brunia & Damen, 1988; Brunia, de Jong, van den Berg-Lenssen, & Paans, 2000), or if both hemispheres are able to modulate the allocation of PA, perhaps in different manners, depending on the configuration (Stephan et al., 2003) and the attentional demands of a given task. In the next sections we will examine these two hypotheses related to hemispheric specialization of PA allocated to a visual stimulus. The first hypothesis states that PA is lateralized in the RH (Unilateral Hemispheric hypothesis, UH). The second hypothesis argues that both hemispheres are implicated in attentional operations computed prior to a stimulus appearance, but with a different role (Differential Hemispheric hypothesis, DH).

3.4.1. *Unilateral hemispheric hypothesis: the modulation of PA is lateralized to the RH*.

Increasing evidence in the literature involves the RH in the attentional preparation to a target stimulus. The hypothesis that PA operations are lateralized to the RH has been examined using different methods in patients with unilateral cerebral damage (Picton, Stuss, Shallice, Alexander, & Gillingham, 2006; Stuss et al., 2005; Vallesi, Mussoni, et al., 2007) and in normal population (Vallesi, McIntosh, Shallice, & Stuss, 2008).

Brunia and Damen (1988) found a RH advantage in allocating PA to a perceptual stimulus that provides feedback information about subjects' response accuracy. They used a task measuring PA to a feedback stimulus called knowledge of results (KR), which provided information about subjects' response accuracy (for more details about this paradigm see

Chapter 2, pp. 34). Using EEG recordings, authors showed that the SPN, a sign of PA, was stronger in the RH. This finding was supported by a PET study showing the activation of PFC, insula, and parietal cortex in the RH when anticipating the KR stimulus (Brunia et al., 2000). But PA is not an all-or-nothing phenomenon. In contrast, PA is assumed to be a modulatory process influenced by subjects' expectations in relation to the temporal and spatial characteristics of a target stimulus.

3.4.1.1. Stimulus predictability and the RH

In the studies of Brunia et al., the KR stimulus had 100% probability of occurrence, meaning that its appearance was highly predictable within a trial. The involvement of the RH in processing events with high predictability has been shown in a study in which split-brain patients and patients with unilateral frontal damage had to predict the forthcoming occurrence of two possible stimuli with different probabilities. The RH of split-brain patients and patients with left frontal damage used a *maximizing* strategy based on the systematic prediction of the most frequent stimulus (Wolford, Miller, & Gazzaniga, 2000). This finding suggests that the RH might base its expectations on the stimulus with higher probability of occurrence, enhancing activity in preparation to that stimulus.

The RH involvement in PA can also be related to the temporal probability of an expected stimulus. For instance, the KR stimulus always occurred within 2 seconds of the subject's response, meaning that it also had a high temporal predictability. The particular role of the RH in processing stimuli with high temporal predictability has been reported in different studies. In an fMRI study, Vallesi et al. (2008) examined the cerebral activations related to the expectation of a stimulus in time. They used a paradigm in which targets could appear at different time intervals within a trial. It has been widely demonstrated that when the time interval in which the target stimulus can appear is variable, RTs are faster at intervals in which the target has the highest probability of occurrence (See Chapter 1, pp. 21). The preparation to respond to the target stimulus presumably increases as its probability of occurrence increases. Vallesi et al. found that frontal regions of the RH were selectively activated in trials in which the target stimulus appeared at the interval with the highest probability of occurrence. Studies in patients with unilateral frontal brain damage found that RH lesions harmed the ability to prepare for the appearance of a target stimulus with high

temporal predictability (Stuss et al., 2005; Vallesi, Mussoni, et al., 2007). Consistent with the result obtained in patients, the momentary interruption of normal activity in frontal regions of the RH was shown to reduce significantly the ability of preparing to the occurrence of a stimulus that is highly predictable in time (Vallesi, Shallice, et al., 2007). The application of TMS over the right DLPFC of healthy participants reduced the behavioral advantage (faster RTs) of responding to a target stimulus with high temporal probability. Thus, these findings outlined the importance of the temporal probability of a target stimulus in the modulation of PA by the RH. The RH might be particularly recruited when subjects prepare for the occurrence of a stimulus with high temporal predictability.

Another useful tool to measure the ability of anticipating the appearance of target stimulus at a certain point in time is the temporal attentional orienting task (see Fig. 5). In an fMRI study, Coull, Frith, Büchel, and Nobre (2000) found that frontal areas of the RH were especially activated when subjects voluntarily allocate attention to a temporal interval in which the target was highly predictable. The DLPFC and ventrolateral prefrontal cortex (VLPFC) of the RH were activated when the target occurred at a longer delay than indicated by the cue. In this type of invalid trials the cue indicated that the target would appear at a short delay (first possible SOA), but it actually appeared at a long delay (second possible SOA). In such a condition, subjects might voluntarily prolong their attention within a trial in preparation of the target. The high probability of the target occurrence at the second delay presumably reinforced preparation. In this condition, the frontal activation of the RH may be related to the enhancement of attention at the second delay owing to the high predictability of the target at that delay.

3.4.1.2. Stimulus timing and the RH

A core operation in PA might be the timing of events. The enhancement of attention in preparation of a target stimulus should involve the estimation of the time interval at which the target occurs. The RH might be essential in the estimation of time intervals (Lewis & Miall, 2006), especially with intervals in the range of seconds (Jones, Rosenkranz, Rothwell, & Jahanshahi, 2004). The right PFC was shown to be especially involved in the representation of the temporal contingencies of past stimuli in working memory (Harrington, Haaland, & Knight, 1998; Rao, Mayer, & Harrington, 2001). Comparing stored representations of intervals in working memory is a necessary process to make, for example, temporal

judgments of visually presented stimulus, and it was shown that the RH outperforms the LH in making such judgments (Funnell, Corballis, & Gazzaniga, 2003).

The existence of a cortical timing network, so-called *when* pathway, lateralized in the RH, particularly involving parietal areas and the DLPFC (Battelli, Pascual-Leone, & Cavanagh, 2007) has been proposed. Specifically in vision the *when* pathway is largely restricted to regions that are also involved in spatial processing. This finding led to the idea that spatial and temporal representations might have similar underlying brain structures.

3.4.1.3. The RH spatiotemporal integration

There is evidence in the literature that spatial factors affect the perception of time and other magnitudes (Bueti & Walsh, 2009; Walsh, 2003). The spatial and temporal representations might share common brain structures, mostly lateralized in the RH (Oliveri, Koch, & Caltagirone, 2009).

Consistent with this proposal, there is a great amount of research supporting an interaction of spatial and temporal information in the human brain (Oliveri et al., 2009). Studies in patients with disabilities in spatial attention after right parietal damage suggested that the RH supports spatial attentional mechanisms that are time-dependent. Lesions of the parietal cortex of the RH in humans can lead to a syndrome known as hemispatial or unilateral neglect. Neglect patients have deficits in orienting attention to the contralateral side of the lesion (LVF after RH damage). This deficit has been generally related to the damage of brain areas related to spatial attention. However, several studies assert that the impairment of other non-spatial cognitive processes can contribute and increase the severity of the spatial disorder (e.g. Robertson et al., 1997).

Husain, Shapiro, Martin, and Kennard (1997) examined the non-spatial temporal dynamics of attention in neglect patients. They were interested in investigating whether there was a temporal component in the spatial deficit of these patients. Neglect patients were presented with a rapid, serial sequence of letters (RSVP task, see Fig. 3), using a variable temporal proximity between them. They had to identify one (control task) or two (dual task) target letters. As mentioned in Chapter 1 (pp. 17), neurologically intact participants were impaired in the identification of the second target if it appeared within 500 ms after the first target. In neglect patients, the *attentional blink* phenomenon was widely increased. When

patients identified T1, they were impaired in detecting T2 for up to 1140 ms afterwards. Such a finding raised the possibility that spatial deficits in attention after RH damage had a significant temporal component.

In a recent behavioral study, Malhotra, Coulthard, and Husain (2009), explored the capacity of neglect patients to sustain attention towards a selected target location over time. They asked patients to perform a task in which they had to report the appearance of a stimulus in two regions of space out of five. The two target locations were specifically cued in advance and subjects had to direct and sustain their attention only to those locations. They found that neglect patients had important difficulties in sustaining attention over the indicated locations, suggesting that the right posterior parietal cortex has a crucial role in sustaining attention to spatial locations over relatively long periods of time. Siéroff, Decaix, Chokron, and Bartolomeo (2007) showed that some but not all left neglect patients had difficulty sustaining attention after a LVF valid cue, even in predictive cueing conditions. These patients, who have preferentially a subcortical (thalamic) lesion, may have some difficulty in PA in the LVF. Moreover, the spatial neglect, as defined by clinical tests, was stronger in these patients compared to patients who were able to sustain attention.

3.4.1.4. Spatio-temporal integration and PA

The integration of spatial and temporal information constitutes a necessary operation of the cognitive system in order to allocate PA to an expected visual stimulus. A common situation in which the system has to integrate spatio-temporal information is the processing of objects in movement. When a target object is not static, the anticipation of the next position in order to follow its trajectory may require the integration of its spatial and temporal characteristics. If the moving object has a spatio-temporal regularity, the attentional system might be able to anticipate its spatial position at a given time because its movement is highly predictable. However, if the movement of the object is not regular, this irregularity might prevent the system from preparing for its next position. Therefore, PA directed to non-static objects may be influenced by the predictability of their trajectories. In an fMRI study, Vallesi and Crescentini (2011) measured the cerebral activations of normal subjects while they monitored the trajectory of an object with apparent movement. Participants were presented with a color dot inside a rounded barrier, and they were instructed to detect the hit of the dot in the inner or outer “crash-barrier” by pressing a button with their right hand. The apparent

movement of the dot was obtained changing its position every 500 ms. The dot moved following four different types of spatial trajectories: regular predictable, regular unpredictable, random and zig-zag (see Fig. 18 for some trajectories examples). They found that parietal and frontal regions in the RH were specifically activated when the relevant object followed a regular predictable trajectory. This result suggests that the RH might be involved in anticipating the spatial and temporal characteristics of a highly predictable event.

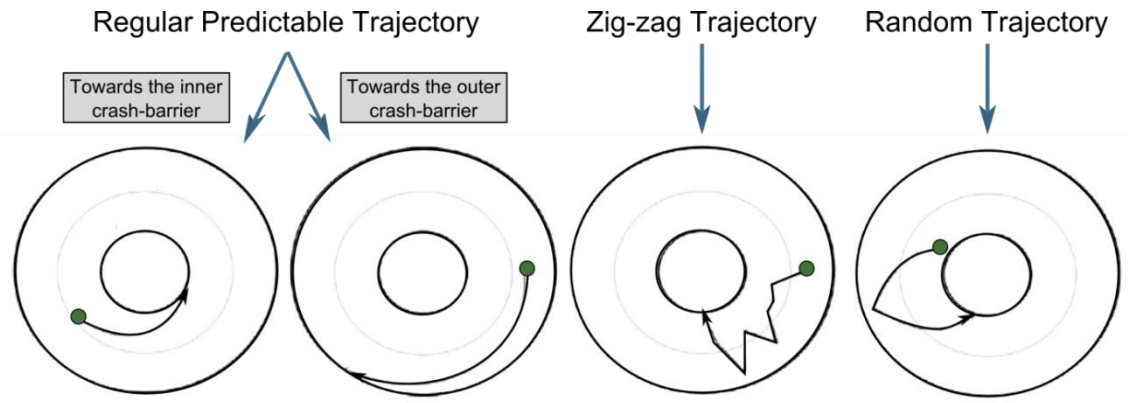

Figure 18: Illustration of some trajectories in the study of Vallesi and Crescentini, (2011). Subjects were instructed to respond as soon as the target (green dot in the example) touched the inner or the outer circles, so-called crash-barriers. The arrows represent the target trajectory in each condition.

Taking these findings together, the RH may have a crucial role in the allocation of PA to an expected stimulus. The amount of PA directed to a target stimulus might be modulated in the RH by the spatial and temporal probabilities of the expected target. The RH might voluntarily enhance attentional activity directed to an expected target stimulus taking into account its high predictability in spatial and temporal dimensions.

3.4.2. *Differential hemispheric hypothesis: both hemispheres participate in the modulation of PA*

According to the DH hypothesis, both hemispheres may participate in the modulation of PA but in a different manner. The involvement of one or the other hemisphere might be related to the task configuration and to the context in which the expected stimulus appears.

The RH was shown to be involved in the enhancement of attention prior to the occurrence of a highly predictable target in spatial and temporal dimensions. In addition to the role of the RH in PA, two attention-related functions of the LH might be important in the preparatory processes: the selection, specifically in difficult situations, and the sensitivity to the frequency of past events.

3.4.2.1. Selection in difficult tasks and the LH

The selection function is related to the attentional demands of the task. Posner and Petersen (1990) suggested that anterior areas of the LH control the allocation of visual attention, when signal selection is necessary. By testing patients with unilateral posterior damage, Rushworth, Nixon, Renowden, Wade, and Passingham (1997) found that LH is implicated in choice reaction time tasks, although both hemispheres are involved in simple reaction time tasks. LH lesions disrupted the ability of selecting a motor response from different alternatives, when these alternatives were defined in advance. Consistent with this finding, TMS over the left but not the right lateral premotor cortex impaired the ability to select a specific movement from other alternatives in a task with several response choices, but not in a simple task with only one response (Schluter, Rushworth, Passingham, & Mills, 1998). Moreover, a PET study revealed that the LH increased its activation when selecting a response from different alternatives regardless of the hand used to make the response (Schluter, Krams, Rushworth, & Passingham, 2001).

Attention selection can often occur at the perceptual level of information processing. In such cases, selection serves to separate relevant from irrelevant information for subsequent processing. In a divided visual field study, Michael and Ojéda (2005) reported a RVF advantage in processing targets that were relatively hard to discriminate form irrelevant distractors, suggesting that the LH may outperform the RH in difficult tasks requiring fine-grained resolution to select relevant target information. There is also evidence supporting a LH advantage in attentional selection occurring in the absence of an over motor response. In an fMRI study, Zhang, Feng, Fox, Gao, and Tan (2004), reported activation in frontal regions of the LH when participants had to select specific items representations from within working memory. In their study, participants were presented with two sets of letters to memorize (study display). Only one of the two sets was relevant to their final response, but they were told to remember both at first. After memorization, participants were cued to select one set

from the two as the target set for a subsequent recognition test. The cued set of letters was presented either in red or in green. The color was related with one of two experimental conditions. In one condition participants had to hold the cued set of three letters as the target set (easy selection). In the other condition they had to discard the cued set and withhold the alternative one (not presented in the cue) as the target set for subsequent processing (hard selection). The association of the cued set colors and the conditions was balanced between subjects. Following the cue, a single probe letter was presented on the screen and participants had to indicate whether the probe was part of the target set (Fig.19). The condition based on discarding the cued set was argued to have a higher involvement of selection because subjects had to inhibit the set of letters presented in the cue and select the alternative set from within working memory. The results of this study showed prefrontal activation of the LH for the hard condition, in which subjects had to select information from within working memory and discard (inhibit) at the same time perceptual distractors. These findings suggests the particular involvement of the LH to select relevant information in difficult situations.

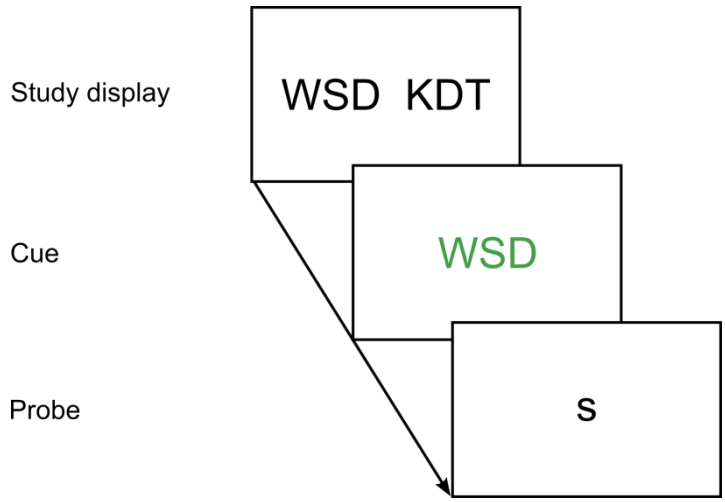

Figure 19: Schematic view of a trial events sequence in the selection task used by Zhang et al. (2004). Each trial began with the presentation of two sets of letters that subjects had to memorize (study display). After a delay, a cue repeating one of the two sets was presented in green (like in the figure) or red. The color indicated whether subjects had to withhold the presented set of letters as the target set (easy selection condition), or discard the cued set and select the non-presented letters as the target set (hard selection condition). The association of the color used in the cue and the condition was balanced between subjects. Following the cue, a probe letter was presented and subjects had to respond whether the letter was in the target set.

3.4.2.2. PA in difficult tasks and the LH

When the selection of a relevant representation becomes more difficult within a task, more attentional control is presumably needed in order to respond correctly. In such difficult situations, the anticipation of the attentional demands might be beneficial for performance as this information can be strategically used to respond to the task at hand. In order to investigate the cerebral basis of this anticipatory process, MacDonald, Cohen, Stenger, and Carter (2000) used a modified version of the Stroop paradigm, in which subjects were given a written instruction before each trial. The instruction indicated the required attentional demands of the forthcoming task: participants were instructed to either respond according to the ink color (high attentional control demands) or word reading (low attentional control demands). The following trial could be congruent or incongruent (see Fig. 6 for examples of congruent and incongruent trials). The left DLPFC was particularly activated following the instruction that indicated the necessity of more attentional control in the upcoming trial (i.e. respond according to the ink color). This lateralized activation was correlated with a reduced interference effect, suggesting that this region might play a preparatory role in attentional control. This preparatory process presumably reduced response conflict and interference. Thus, the left DLPFC was argued to have a crucial role in representing and actively maintaining the attentional demands of the task and it was associated with strategic control processes in preparation of difficult situations.

In a similar fMRI study, Luks et al. (2007) used a cued flanker task to examine the brain regions activated in anticipation of situations with different levels of difficulty. In their study, each trial could be preceded by a 100% informative (valid) cue, indicating whether the selection of the target in the next trial would be easy (congruent trial) or hard (incongruent trial), or by neutral cues with no specific information. It was reasoned that in the informative condition, subjects might be able to select and deploy a preparatory strategy to maximize performance for each level of difficulty (Luks et al., 2007). The findings of this study demonstrated that the presentation of informative cues selectively activated the DLPFC and the intraparietal sulcus (IPS) regions of the LH. This result suggests that, when the upcoming attentional demands of a task are informed in advance, a network involving frontal and parietal cortex, particularly lateralized in the LH, mediates the modulation of attentional resources in preparation for a specific level of difficulty.

3.4.2.3. The LH and the processing of stimuli probability

The amount of PA directed to a specific target is also related with their expected probability of occurrence. The probability of a target occurrence can be strategically used to distribute attentional resources. Detecting changes in the probability of events is a useful capacity to adapt behavior accordingly, and the LH might have an important role in processing probabilities.

Learning stimuli probability is a necessary operation to modulate the distribution of attentional resources according to such probabilities. Kincses, Antal, Nitsche, Bártfai, and Paulus (2004) examined the effect of modulating the activity of different brain regions with tDCS while normal subjects performed a probability learning task. The task of participants consisted in responding whether a specific combination of geometric forms predicted rainy or sunny weather. The different combinations were probabilistically related to a particular weather outcome and subjects had to implicitly learn the probability of a specific geometric combination and one or the other outcomes. They found that anodal stimulation over the left PFC improved the ability of learning the probability of a perceptual stimulus with a particular outcome. This finding demonstrates that the left PFC has an important role in probability learning and it suggests that the LH might strategically use these probabilities to accordingly prepare for future events.

3.4.2.4. The distribution of PA according to probabilities and the LH

The probability of expected events can be strategically used to control the allocation of PA. It has been argued that the LH might selectively allocate attentional resources prior to the appearance of stimuli according to their expected probability. Wolford et al. (2000) have shown that the LH of split brain patients and patients with unilateral frontal damage used a specific strategy when predicting the occurrence of two possible stimuli in the future. Unlike the RH, the LH based its choices on the frequency of each stimulus that occurred in the past. In other words, the LH used a *frequency matching* strategy. This hemispheric strategy was also examined in a behavioral study with normal participants. Wolford, Newman, Miller, and Wig (2004) tested the involvement of each hemisphere of neurologically intact individuals in a guessing task. They used a competing-task paradigm in which the main task (guessing task)

was performed in the presence of distracting (competing) tasks. The distracting tasks could primarily engage LH or RH resources. It was hypothesized that the competing task that undertake primarily LH resources would interfere with *frequency matching*, while the other task that engaged RH resources would not. They found that subjects tended to maximize their guess when the competing task involved LH resources, but they maintain *frequency matching* when the task involved RH resources. According to these findings, LH resources might be crucial in the deployment of a *frequency matching* strategy when anticipating the occurrence of two possible events with different probabilities. The LH might examine the frequency of occurrence of each possible event and match the preparation for the upcoming event to its expected probability.

The hemispheric strategies in anticipation of future events was also examined using tDCS methods (Hecht, Walsh, & Lavidor, 2010). The left and right DLPFCs were stimulated while participants were engaged in a guessing task. The results showed that all participants tended to use a *frequency matching* strategy whatever the type (anodal, cathodal) or the site (LH, RH) of stimulation. However, when anodal tDCS was applied to the DLPFC of the LH and cathodal tDCS to the homologue region in the RH, participants selected faster the most frequent alternative. The higher probability of the most frequent stimulus might have modulated the amount of attentional activity directed to it prior to its occurrence. Increasing the amount of PA directed to an expected event may decrease the time taken to make a decision in anticipation of its appearance. Hence, this finding suggests that the left DLPFC might have a role in modulating the processing speed to select a stimulus according to its expected probability.

The probability of a target appearance in a certain spatial location may modulate the allocation and distribution of PA in the visual field. Robertson, Lamb, and Knight (1988) explored the capacity of brain hemispheres in controlling the modulation of the attentional distribution in space when manipulating events' probability. Subjects with left or right temporal-parietal damage and controls were presented hierarchical stimuli with global and local levels (see Fig.17) and were asked to detect a target appearing at one level or the other. Authors manipulated the probability of a target appearance at a certain level. For instance, in the global-bias condition, the target appeared at the global level 75% of the time, and in the local-bias condition, the target appeared at the local level 75% of the time. The results of this study showed that normal subjects and participants with RH lesions were able to direct more attention to the target at the level that was most likely to appear. However, the group of

participants with a parietal lesion in the LH did not show such an advantage of processing the target at the level with higher probability, whatever the size of the target (global or local). This finding suggests that the LH might be crucial to control the allocation of attentional resources, taking into account the probability context in which stimuli appear.

In summary, PA might not be exclusively lateralized to the RH (UH). In contrast, both hemispheres may be involved in the modulation of PA to an expected stimulus, but each hemisphere may have its own strategy to allocate PA towards expected events (DH). The involvement of one or the other hemisphere in PA may depend on the spatial and temporal context in which stimuli occur and it may also depend on the complexity and the attentional demands of the task to be performed.

3.5. Conclusion

Brain hemispheric specialization of different cognitive functions has been the object of a long debate in cognitive research. Several methods were developed to study the capacities of each hemisphere in visual attention. The selection of some specific visual stimuli might be lateralized, suggesting hemispheric specialization in processing certain type of visual information. The attentional ability to prepare for the appearance of an expected stimulus may also differ between hemispheres. However, there is no consensus in the literature concerning hemispheric differences in PA. One hypothesis states that PA is lateralized to the RH (UH). An alternative hypothesis argues that both hemispheres are involved in the modulation of PA to an expected stimulus, but in a different manner (DH). The RH might modulate PA according to the high predictability of a relevant target stimulus in spatiotemporal dimensions. The LH might modulate PA according to the expected probability of different events, taking into account their frequency in the past. The attentional demands required to select relevant from irrelevant information might also modulate PA in the LH. Thus, according to the DH hypothesis, the implication of either hemisphere in PA processes may depend on the task configuration and on the probability context in which stimuli are expected to occur.

PRESENTATION OF THE EXPERIMENTAL STUDY

The human capacity to allocate attention prior to the appearance of an expected stimulus allows faster and more effective responses to that stimulus. PA is a crucial aspect of attentional control that gives the possibility to adapt behavior according to the expected information. The neural bases underlying PA processes have been widely studied using different methods in patients and neurologically intact populations. Several brain regions including cortical and subcortical areas constitute the neural network involved in PA. The goal of this thesis is to evaluate the role of each cerebral hemisphere in PA. Some studies proposed that the attention system controlling the allocation of PA is lateralized to the RH. This hypothesis (UH) highlights the crucial role of the RH in prolonged attention (like sustained attention) in general, or, more specifically, in directing PA to an expected stimulus. However, several findings in the literature suggest that the LH might also be able to allocate attentional resources prior to the presentation of a stimulus in some situations. According to this second hypothesis (DH), both hemispheres play a specific role in the modulation of PA to an expected event and the implication of one or the other hemisphere would depend on the requirements of the task to be performed and the probability context in which the different stimuli are embedded. Each hemisphere might have a particular strategy when preparing for the appearance of events with different probabilities. The RH might modulate PA according to highly probable stimuli in spatiotemporal dimensions, allocating a maximum of resources to the most probable stimulus (*maximizing* strategy). The LH might modulate PA according to the expected probability of different stimuli, distributing resources as a function of their frequency in the past (*frequency matching* strategy). Thus, there is no general agreement about whether PA is lateralized to the RH or relates to both hemispheres operations.

The APT, proposed by LaBerge et al. (2000), has proven to be a useful tool in measuring the modulation of PA directed to a spatial location, as a function of the frequency of events. We developed different lateralized versions of the original APT, or LAPT, using the divided visual-field paradigm to evaluate the modulatory capacity of each hemisphere. The rationale is that visual field differences in modulating PA may refer to hemispheric differences in PA. Each LAPT version varied the temporal and spatial characteristics of

stimuli in order to be adapted to the theoretical questions. The type of distractor presentation (central or peripheral) and the information given to participants about the proportion of distractors within a block of trials was also manipulated.

The expected probability of stimuli might influence the intensity of PA directed to each of them. In the APT, the relative frequency of the targets and stimuli has been manipulated (LaBerge et al., 2000). However, while the target frequency manipulation affects both perceptual and motor processes (Experiment 4), authors assumed that the distractor frequency manipulation mainly affects perceptual processes (Experiments 1 to 3). In the APT, the RTs to the target increased as a function of the relative frequency of distractors. The intensity of attentional activity directed to the target location prior to its occurrence was presumably modulated by the expected probability of a distractor at a perceptual level. The first experimental study (Chapter 4) was designed to examine this modulatory process in each visual field / brain hemisphere.

The temporal probability of an expected stimulus may also modulate the attentional activity directed to this stimulus prior to its occurrence. Decreasing the temporal probability of a target stimulus at a specific time interval decreases its temporal predictability, thus influencing its expectation within a trial. The second experimental study (Chapter 5) was designed to test the role of stimuli temporal probability in the allocation of PA by each hemisphere.

Previous information about the proportion of distracting events may modulate expectations in the upcoming block of trials. The lack of this information may influence the strategy chosen to regulate PA directed to the relevant event. The third experimental study (Chapter 6) assessed the modulation of PA by each hemisphere when there was no advance information about the proportion of distractors in the upcoming block of trials, contrary to the first experimental study. The motor demands of the task may also have a role in the selection of a strategy to modulate preparation. In Chapter 6, the role of the motor demands of the task in the strategy developed by each hemisphere was further explored.

The intensity of attention directed to a spatial location prior to a target appearance in that location can be modulated by an instruction (LaBerge et al., 2000; Experiment 2). Instructing participants to reinforce their attention to the target location may increase the amount of PA directed to that location from the beginning of the trial, decreasing the effect of distractors. The fourth experimental study (Chapter 7) was designed to examine the capacity of each hemisphere to reinforce the intensity of PA directed to a target location by means of an instruction.

Finally, the difficulty in discriminating the target from the distractor location might influence the preparatory strategy to respond to the target. The spatial proximity of targets and distractors was shown to influence the difficulty in responding to the task. The final experimental study (Chapter 8) evaluated PA in conditions in which the discrimination of target location from distractor location had different levels of difficulty. More precisely, the capacity of each hemisphere to allocate PA to a spatial location was tested when the target/distractor spatial locations overlapped and when they did not.

PART 2: Experiments

CHAPTER 4 – Effect of distractor probability in the modulation of PA by the brain hemispheres

4.1. General presentation of the study

The intensity of attention directed to an expected target stimulus prior to its onset was shown to be related with the relative frequency of that stimulus in the past (LaBerge et al., 2000). If the expected probability of the target occurrence is high the intensity of PA should be also high. When a possible distracting stimulus appears in the time interval at which a subject prepares to process a target, it might act as a competitor for PA. The increase of the distractor probability might relatively decrease the amount of attentional activity directed to the target stimulus before its appearance. Thus, the allocation of PA is not a static operation but a continuously variable modulatory process that is highly influenced by the expected probability of possible events. The aim of this first study was to examine this modulatory process in the two brain hemispheres.

There is not a unitary consensus about the role of each hemisphere in the modulation of PA. A first hypothesis states that PA is lateralized to the RH (UH hypothesis). Different studies reported the activation of several RH regions in anticipation of an expected visual stimulus, suggesting the RH specialization in PA processes (Brunia & Damen, 1988; Brunia et al., 2000). A second hypothesis states that both hemispheres might be involved in the modulation of PA to an expected stimulus, but in a different manner (DH hypothesis). The different modes of modulating PA by each hemisphere may be related with the processing of probabilities.

The RH may be especially involved in the anticipation of a highly predictable visual stimulus. The RH was shown to be particularly active when processing a visual stimulus with high regularity and temporal predictability (Vallesi & Crescentini, 2011). When the temporal probability of the relevant stimulus is variable within a trial, the RH activation was related with the appearance of the stimulus at the interval in which it had the highest probability of occurrence (Vallesi et al., 2008). This activation was correlated with faster RTs at those intervals, suggesting a RH role in the speed of processing a stimulus with high temporal

probability. It was proposed that the RH voluntarily enhances attentional activity directed to a temporal interval in which the appearance of a target event is highly predictable (Coull et al., 2000). The specific role of the RH in processing highly probable events might be related to its strategy when anticipating the appearance of events with different probabilities. The RH systematically anticipates the stimulus with higher probability of occurrence, meaning that it uses a *maximizing* strategy (Wolford et al., 2000). Therefore, the RH modulation of PA would be associated with the processing of highly predictable events, particularly with these events occuring with high temporal probability.

The LH may differ to the RH in the strategy used to anticipate the appearance of stimuli with different probabilities. The LH anticipates either stimuli according to their frequency in the past, meaning that it uses a *frequency matching* strategy (Wolford et al., 2000). The strategy used by the LH when anticipating future events might be related to the general role of this hemisphere in probability learning (Kincses et al., 2004). The LH might use the information accumulated from the frequency of events to distribute attentional resources according to their expected probability (Robertson et al., 1988). Consistent with this proposal, the stimulation of neural activity in frontal areas of the LH modulated the speed of processing stimuli with different probabilities. More precisely, more frequent stimuli were processed faster than less frequent ones (Hecht et al., 2010). Thus, the LH might also be involved in PA process, modulating the attentional activity directed to stimuli prior to their occurrence according to their expected probability.

The present study was designed to examine the role of both hemispheres in the modulation of the intensity of PA directed to a target location. The APT (LaBerge et al., 2000) demonstrated to be a useful test to measure the human capacity of modulating the amount of PA directed to a target location while the probability of a distractor appearance varied in several blocks. With the APT we can investigate the ability to regulate the preparatory attentional activity directed to an event according to its expected probability. We developed a lateralized version of the APT, called the LAPT (for *Lateralized Attentional Preparation Test*), using the divided visual field method. In the LAPT, targets were lateralized and the distractor was centered. We considered response latencies to LVF targets as a direct measure of the generation of PA by the RH, and response latencies to RVF targets as a direct measure of the generation of PA by the LH. With the LAPT, we measured the modulation of attention directed to the target location by each visual field/hemisphere prior to its occurrence when the probability of a distractor expectation varied in several blocks. The

distractor probability increased along three consecutive blocks of trials, with 0%, 33%, and 67% of distractors, respectively. The reason why we did not use as many blocks of trials as in the APT experiment (four blocks in the APT; LaBerge et al., 2000) is because we did not want to have an experiment with a long duration. The number of blocks was reduced in order to compensate the higher number of trials in each block. Indeed, the number of test trials in each block was higher in the LAPT (84 trials) than in the APT (60 trials), because PA is measured in each visual field in the LAPT, instead of only in the foveal area, like in the APT. PA requires a high amount of resources, and prolonging the total experiment duration may have affected PA. Moreover, a version of the APT with only three blocks of trials has shown comparable effects of distractor frequency as the version with four blocks (Auclair et al., 2005; Siéroff et al., 2004). In the LAPT, participants were explicitly informed about the proportion of distractors before the beginning of each block. The temporal probability of the target appearance was constant between trials. Precisely, when a target occurred within a trial, it always appeared at a "long" interval, having a high temporal predictability.

In Experiment 1, we used a location task in which subjects had to respond to the target in the RVF or LVF using the right or the left hand, respectively. In this task, the same hemisphere receiving the perceptual input produced the response to the target, leading to the maximal independence of information processing in the hemispheres, because no callosal transfer was needed. However, in a location task, the LH selection process might be activated because subjects have to select from different response alternatives (Rushworth et al., 1997; Schluter et al., 2001, 1998). Thus, to minimize the LH recruitment by the response selection process, we conducted a second experiment (Experiment 2), in which subjects had to simply detect the target, whatever its location. To avoid changes in the level of response bias across conditions (e. g. LaBerge et al., 1969), a target occurred in 50% of trials, whatever the task.

With this paradigm, we addressed the question of whether PA is lateralized to the RH or whether each hemisphere modulates PA to a visual location differently. If PA is lateralized to the RH, we should find an advantage for targets appearing in the LVF. More specifically, there should be a smaller sensitivity to the distractor probability, with faster RTs to the target in the LVF, indicating that the RH is best suited to enhance attention toward the target in preparation to its appearance (Fig. 20A). If both hemispheres play a different role in PA we should obtain a different results pattern in each visual field as a function of the probability of events (Fig. 20B). The LH may match its expectation strategy with the frequency of targets and distractors (*frequency matching* strategy). As only the distractors frequency was varied in

the different blocks of trials, we should obtain a gradual increase of RTs in the RVF as a function of distractor probability. The RH may base its expectation strategy on the high predictability of a target occurrence within a trial (*maximizing* strategy). Since the RH is sensitive to events with high temporal probability we should find certain regularity in RTs for targets in the LVF across block of trials owing to the high predictability of the target at long intervals. Concerning the task to be performed, it was hypothesized that a location/selection task should give an advantage to the RVF/LH compared to the detection task.

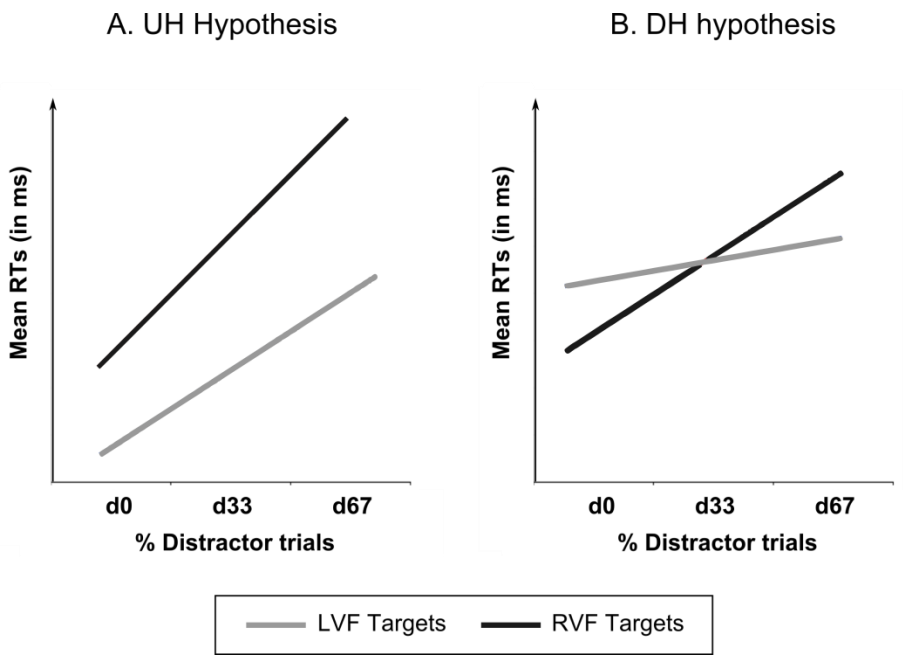

Figure 20: Hypothetical slopes for targets appearing alone within a trial in the left visual field (LVF) and in the right visual field (RVF). A. Unilateral Hemispheric (UH) hypothesis. B. Differential Hemispheric (DH) hypothesis. See text for details.

4.2. Experiment 1

4.2.1. *Presentation of the experiment*

In this experiment we used the LAPT with a location/selection task, in which responses to RVF targets are made by the right hand, and responses to LVF targets are made by the left hand. We were interested in the effect of the probability that a distractor might

appear in the preparatory phase preceding the target appearance. As in the APT, there were two types of trials containing a target: trials in which only a target occurred, and trials in which the target was preceded by a distractor. We assessed the modulation of PA in each hemisphere by measuring the increase of RTs as a function of the percentage of distractors (absent, rare, frequent) in the blocks of trials, specifically in those trials in which no distractor actually occurred before the target, as in the APT (LaBerge et al., 2000). In those trials, the expectation of a distractor may compete with PA to an upcoming target, influencing the intensity of attention directed to the target prior to its occurrence. After the appearance of a distractor within a trial, there is no longer expectation concerning the distractor, because distractors occur only once in a trial. Therefore, a variation of RTs as a function of distractor probability is not particularly expected for targets following a distractor.

4.2.2. *Methods*

Participants. Forty students (12 men and 28 women) of the Institut de Psychologie at Paris Descartes University (M_{age} = 21.2 years, *SD* = 2.5; age range: 18-30 years) participated in Experiment 1. They had normal or corrected-to-normal vision and no psychiatric or neurological history, learning disability or attentional deficit, as assessed by self-report. They were all right-handed (*M* = 82), as evaluated with the Edinburgh Handedness Inventory (Oldfield, 1971). All participants provided informed consent and received course credits for participating in the experiment.

Stimuli. Participants were placed at a distance of 57 cm from the screen. The stimulus display consisted of three empty boxes whose side width was 0.8° of visual angle (8 mm). They were arranged horizontally and centered on the middle of the screen. Boxes were separated from each other by a space of 1.2° of visual angle (12 mm), and the total display subtended 4.8° of visual angle (4.8 cm). The target consisted of a black square of 0.7° of visual angle (7 mm), and could appear in one of the two lateral boxes. The distractor was represented by the same black square appearing in the central box. The distance between the center of the screen and the center of the target subtended 2° of visual angle. This means that the eccentricity of the target (distance between the center of the display and the closest extremity of the target) was 1.65°.

Procedure and apparatus. Stimuli presentation and response data collection were controlled using E-Prime 2.0 software (Psychology Software Tools, Pittsburgh, PA), running

under Window XP on a DELL Latitude 6500 laptop, with a 15.4’’ screen and a resolution of 1920 x 1200 pixels.

The stimuli presented on a trial are shown in Figure 21. Each trial began with the presentation of the three empty boxes in the center of the screen, acting as a warning signal. The target appeared on 50% of the trials, 1800, 2000 or 2200 ms after the warning signal, and remained on the screen for 200 ms. Depending on the trial type, the target would occasionally be preceded by a distractor presented for 200 ms, and appearing 600, 1000 or 1400 ms after the warning signal presentation and, respectively, 1200, 1000 or 800 ms before the target (when it occurred). The three empty boxes remained on the screen until the target presentation was achieved or after a similar delay when no target was presented. The inter-trial interval was 500 ms. In the absence of response, the next trial was automatically triggered 2000 ms after the disappearance of the three boxes.

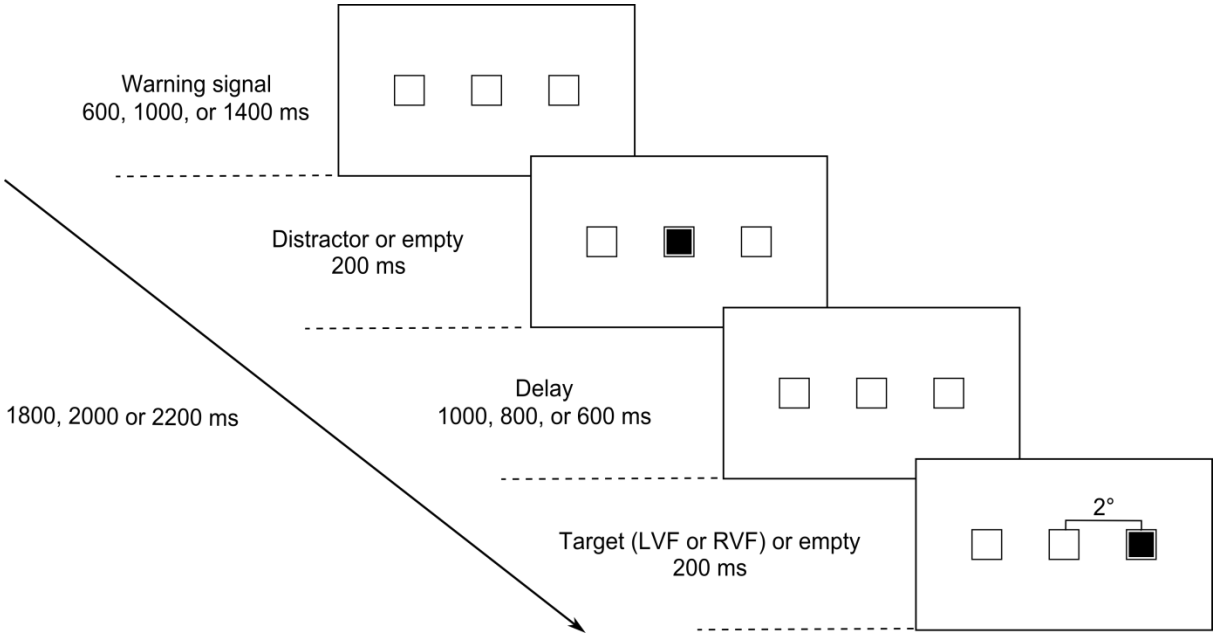

Figure 21: Example of the sequence of stimuli presented in a trial of Experiment 1. The target display showed a black square equally often in the right visual field (RVF) or in the left visual field (LVF).

There were four types of trials: (1) the blank trials in which only the three empty boxes were presented for 2s approximately and then disappeared; (2) the target-only trials (TO trials) in which a target was not preceded by a distractor; (3) the target-following-distractor

trials (TFD trials) in which the presentation of a distractor was followed by the appearance of a target; (4) the distractor-only trials in which the distractor was not followed by a target.

Three experimental blocks of 84 trials each were presented to participants in one session. In each block, 72 randomized test trials were preceded by 12 practice pseudo-randomized trials containing the same proportion of distractor trials than the remaining trials of the block. This was done to prepare the participants to the distractor frequency. The percentage of distractor trials varied: 0% in the d0 block, 33% in the d33 block, and 67% in the d67 block. The d0 block did not contain distractors, whereas a distractor appeared in 24 and 48 trials in d33 and d67 blocks, respectively. The probability of the target occurrence within each block of trials was of 50%. When a distractor occurred in a trial, it was followed by a target 50% of the time and by the three empty squares the other 50% of the time. As in the APT, the three blocks always appeared in the same order (d0, d33, and d67), and were preceded by a 20-trial practice block using a percentage of distractor equal to 50%. The role of the practice block was to make participants familiar with the display and the task.

Table 1

Frequencies of trial types within a block of trials for each visual field (LVF, RVF)

	Percentage of distractor trials					
	0		33		67	
Trial type	LVF	RVF	LVF	RVF	LVF	RVF
Blank	36		24		12	
Target-only	18	18	12	12	6	6
Target-following-distractor	0		6	6	12	12
Distractor-only	0		12		24	

Participants were instructed to fixate the central box during the whole trial, and to respond to the target as quickly and accurately as possible. Studies have shown that subjects can accurately maintain fixation when explicitly encouraged by an instruction (e.g. Posner, Nissen, & Ogden, 1978). With the brief exposure duration of stimuli in the LAPT (200 ms), participants should not have enough time to initiate an eye movement after a stimulus presentation. However, participants could still initiate an eye movement before the stimulus presentation (anticipatory saccades). In order to reduce anticipatory saccades in visual field

studies, Bourne (2006) recommended randomizing visual field of presentation to prevent participants to predict the visual field of presentation of stimuli before its appearance. Thus, in the LAPT, the side of the target location (left or right box) was randomized within a block of trials. Besides, it has been shown that even if participants are allowed to make eye movements towards stimuli in a task that do not require perceptual discrimination, they suppressed them after a few trials because they recognize that eye movements are effortful and did not help performance (see Posner, 1980).

The task was a location task. Participants were required to press the "s" key on a French keyboard with their index finger of the left hand when the target appeared within the left lateral box, and press the "m" key (equivalent to the ";" key of an English keyboard) with their index finger of the right hand when the target appeared in the right lateral box. The keys where marked with color patches. Participants were also instructed to not respond when the black square appeared in the center box (distractor). They were informed before each block about the proportion of distractors (hereafter *D-explicit* instruction), but not about the exact percentage. Before the d0 block, the experimenter said: "there are not many black squares in the central box, and maybe none, in the upcoming block of trials". We said "not many" instead of "no" to catch part of the attention of subjects to the central location. Before the d33 block, the experimenter said: "there are a few black squares in the central box in the upcoming block of trials". Before the d67 block, the experimenter said: "there are more black squares in the central box in the upcoming block than in the last block of trials".

4.2.3. *Results*

Mean RTs on TO and on TFD trials are shown in Figure 22. See Table 2 for the complete RTs data.

Table 2

Mean response times in milliseconds and standard deviations (in parentheses) for target-only trials (TO) and target-following-distractor trials (TFD) of Experiments 1 and 2, for each visual field (LVF, RVF) in d0, d33, and d67.

Experiment number	VF	TO			TFD	
		d0	d33	d67	d33	d67
Experiment 1	LVF	355 (59)	417 (73)	418 (81)	365 (73)	361 (67)
	RVF	345 (58)	400 (60)	422 (75)	345 (65)	342 (59)
Experiment 2	LVF	339 (55)	448 (76)	449 (81)	383 (83)	372 (70)
	RVF	335 (61)	444 (69)	474 (81)	380 (95)	368 (67)

TO trials

We were interested in the effect of the mere probability that a distractor may appear. Thus, we analyzed the RTs to the target in TO trials, in which the distractor did not appear, but was expected to occur. Repeated measures ANOVA were calculated on mean RTs, with distractor percentage (0% or d0, 33% or d33, 67% or d67) and visual field (LVF, RVF) as within subjects' factors.

There was an effect of distractor percentage, $F(2, 78) = 54.41$, $p < .001$, $\eta_p^2 = .58$, indicating an increase of RTs when the percentage of distractor trials increased, as in the APT (LaBerge et al., 2000). The slight difference between the RVF (389 ms, *SD* = 72) and the LVF (397 ms, *SD* = 77) was not significant, $F(1, 39) = 3.09$, $p = .087$. However, the interaction Visual field x Distractor percentage was significant, $F(2, 78) = 3.62$, $p = .031$, $\eta_p^2 = .08$, indicating that while RTs increased gradually as the probability of distractors increased in the RVF (d0 = 345 ms, *SD* = 58; d33 = 400 ms, *SD* = 60; d67 = 422 ms, *SD* = 75), RTs increased between the d0 (355 ms, *SD* = 59) and the d33 (417 ms, *SD* = 73) blocks but not between d33 and d67 (418 ms, *SD* = 81) blocks in the LVF. Planned comparisons revealed that RTs were significantly slower in d67 than in the d33 in the RVF, $F(1, 39) = 9.21$, $p = .004$, $\eta_p^2 = .19$, although no significant difference was found in the LVF, $F(1, 39) = 0.03$, $p = .873$. The analysis of the RVF data indicate that mean RTs increased linearly with the percentage of distractor trials, $F(1, 39) = 68.7$, $p < .001$, $\eta_p^2 = .64$ (The linear model explained 94% of the between-groups variance). Planned comparisons also indicate a trend towards faster RTs in the RVF in d0, $F(1, 39) = 3.92$, $p = .055$, $\eta_p^2 = .09$, faster RTs in the RVF in d33, $F(1, 39) = 12.91$, $p < .001$, $\eta_p^2 = .25$, and no significant difference in d67, $F(1, 39) = 0.19$, $p = .665$.

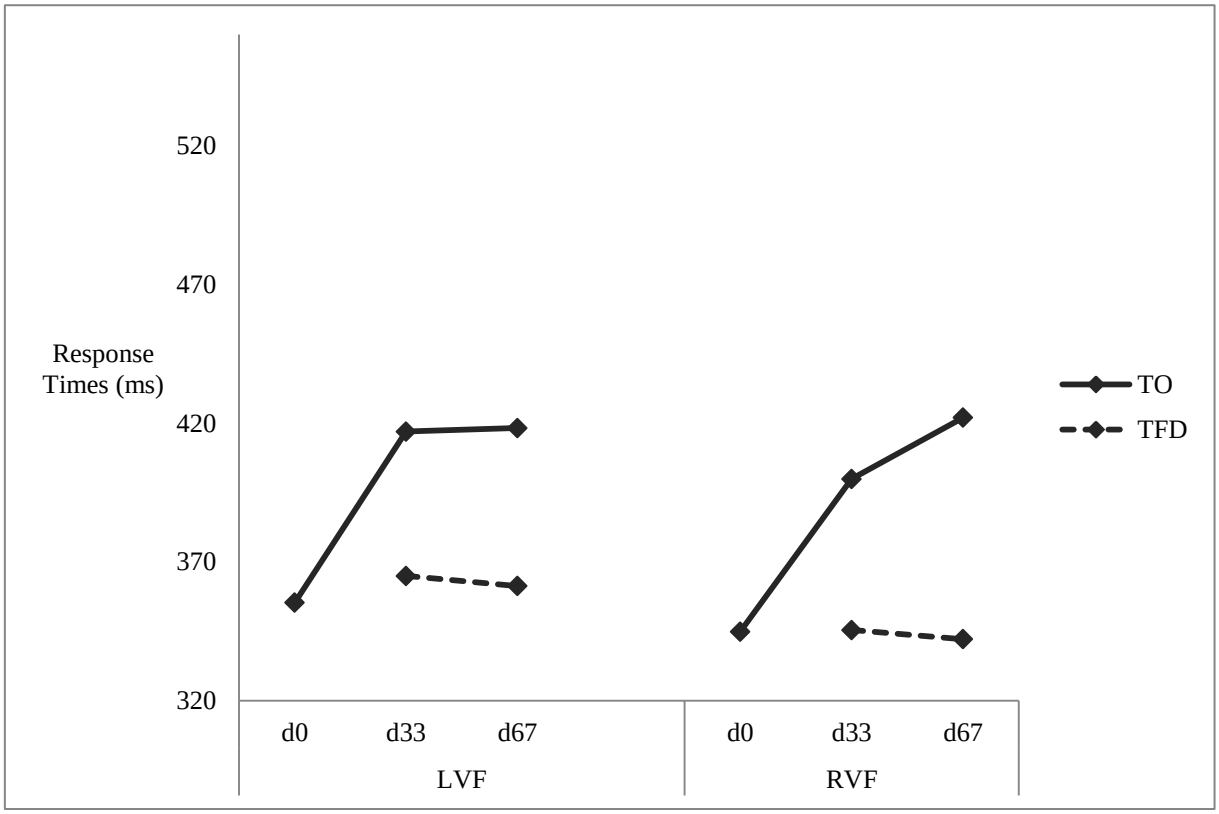

Figure 22: Mean response times in milliseconds (ms) to target-only trials (TO) and to target-following-distractor trials (TFD) in the left visual field (LVF) and in the right visual field (RVF) in Experiment 1.

We evaluated the influence of distractors on the attentional ability of participant to prepare to the target by calculating the RTs slope as a function of the percentage of distractors in a block of trials (using the equations for least squares slope estimation given in LaBerge & Brown, 1986). We carried out an ANOVA on these slope values with visual field (LVF, RVF) as within subjects' factor. There was a slightly larger slope of RTs in the RVF (1.27, *SD* = 0.91) than in the LVF (1.14, *SD* = 0.93), but this difference was not significant, $F(1, 39) = 1.21$, $p = .277$.

TFD trials

Repeated measures ANOVA were calculated on mean RTs, with distractor percentage (33% or d33, 67% or d67) and visual field (LVF, RVF) as within subjects' factors.

The only significant main effect was visual field, $F(1, 39) = 12.99$, $p < .001$, $\eta_p^2 = .25$, indicating faster RTs in the RVF (344 ms, *SD* = 62) than the LVF (363 ms, *SD* = 70). There

was no effect of distractor percentage, $F(1, 39) = 0.45$, $p = .508$, and the interaction did not reach significance, $F(1, 39) < 0.01$, $p = .950$.

Error data

We also measured the number of omissions and false alarms. The mean percentage of omissions was 0.25 %, and the mean percentage of false alarms was 0.17%. As the frequency of errors was negligible, no further analysis was carried out with these data.

4.2.4. *Discussion*

The main finding in Experiment 1 was a different pattern of RTs in the LVF and the RVF when the target appeared alone (TO trials). Before the appearance of a target or a distractor in a trial, the intensity of PA directed to the target was modulated by the amount of expected events within a block, but this modulation differed in each visual field, thus in each hemisphere. This finding is in accordance with the DH hypothesis. For RVF/LH targets, there was a gradual increase in RTs when the likelihood of a distractor appearance increased. Augmenting the frequency of a distractor occurrence increases the competition of the distractor with the target for PA. Thus, the LH might modulate PA by using some *frequency matching* strategy, taking into account the expected frequency of target as well as distractor events, in agreement with the results of guessing experiments (Wolford et al., 2000).

For LVF/RH targets, RTs were affected by the possible occurrence of a distractor, as shown by the difference between d0 and d33 blocks, but were relatively independent of the exact probability of the expected distractor, as shown by the lack of difference between d33 and d67 blocks. The question is whether this pattern of result can be explained by the *maximizing* strategy proposed by Wolford et al. (2000). We cannot answer positively from the sole results from this experiment. First, in none of the blocks, RTs were faster in the LVF than in the RVF. On the contrary, RTs were faster in the RVF in d33 block. Second, there was an effect of the presence of distractors in the LVF as well as in the RVF (difference between d0 and d33 blocks), even though there was no effect of the frequency of distractors in the LVF. A possibility is that slower RTs in the LVF in some blocks are caused by the location task, which induces a selection processes related to the LH (Rushworth et al., 1997). To answer this question, we conducted a similar experiment with a different task (see Experiment 2).

Second, there was an effect of the presence of distractors in the LVF, even though there was no effect of the frequency of distractors. It is possible that a maximizing strategy is only partly efficient with our method. Indeed, it might be very difficult to totally ignore the distractor, especially because it is presented in the central box. The question of knowing what exactly is maximized by the RH still stands. In Experiment 1, the difference of delay between distractor and target occurrence was relatively easy to notice for the observers. Targets and distractors never appeared with the same delay after the warning signal: there was a restricted delay in which a distractor may appear, between 600 and 1400 ms (hereafter short delay), followed by a restricted delay in which the target may appear, between 1800 and 2200 ms (hereafter long delays). Even though the target did not occur in each trial (only 50%) it always occurred at long delays when it occurred. Thus, the results obtained for LVF targets in Experiment 1 suggest that the RH somewhat maximizes the enhancement of PA at the delay in which targets are highly predictable.

After the appearance of a distractor within a trial, subjects only expect for the target to occur. Therefore, in TFD trials, the distractor is not a competitor for PA, and it can act as a "reset" signal or a cue indicating that the target is about to appear (LaBerge et al., 2000). Consequently, as in the APT, there was no effect of distractor percentage. However, we obtained a visual field effect with faster RTs in the RVF. Although sustained attention has repeatedly been associated with the RH (see Posner & Petersen, 1990), lateralized activations to the LH have also been found when a central warning cue precedes a target by a short interval, specifically when this cue does not give any indication about the target location (Coull et al., 2000; Fan et al., 2005). Thus, the advantage of RVF in TFD trials might be explained by the LH involvement in processing the warning cue. It is also possible that the implication of the LH was strengthened by the location/selection task performed throughout this experiment.

4.3. Experiment 2

4.3.1. *Presentation the experiment*

In Experiments 1, the LH involvement in a task in which subjects have to select a response from different alternatives may explain why RTs are faster in the LVF for d33. In Experiment 2 we used a detection task with only one possible response. Consequently, the LH control over the task should be reduced. This change in the task should allow a better evaluation of the role of each hemisphere in the modulation of PA *per se*, independently of task demands, specifically in the selection component.

4.3.2. *Methods*

Participants. Forty students (12 men and 28 women) of the Institut de Psychologie at Paris Descartes University (M_{age} = 21.8 years; *SD* = 3.7; age range: 18-35 years), different from Experiments 1, participated in Experiment 2. They had normal or corrected-to-normal vision and no psychiatric or neurological history, learning disability or attentional deficit, assessed by self-report. They were all right-handed (*M* = 90), evaluated with the Edinburgh Handedness Inventory (Oldfield, 1971). All participants provided informed consent and received course credits for participating in the experiment.

Stimuli. Stimuli were the same as in Experiment 1.

Procedure. Experiment 2 was the same to Experiment 1 with the exception of the task performed by participants. In this experiment, participants were required to make a unimanual response to the target with their index finger, and to respond as soon as the target appeared (detection task). The response key was placed at midline and the hand of response was balanced between subjects.

4.3.3. *Results*

Mean RTs on TO and on TFD trials are shown in Figure 23. See Table 2 for the complete RTs data.

TO trials

A repeated measures ANOVA was calculated on mean RTs, with hand of response (left hand, right hand) as between subjects' factor, and distractor percentage (d0, d33, d67) and visual field (LVF, RVF) as within subjects' factors.

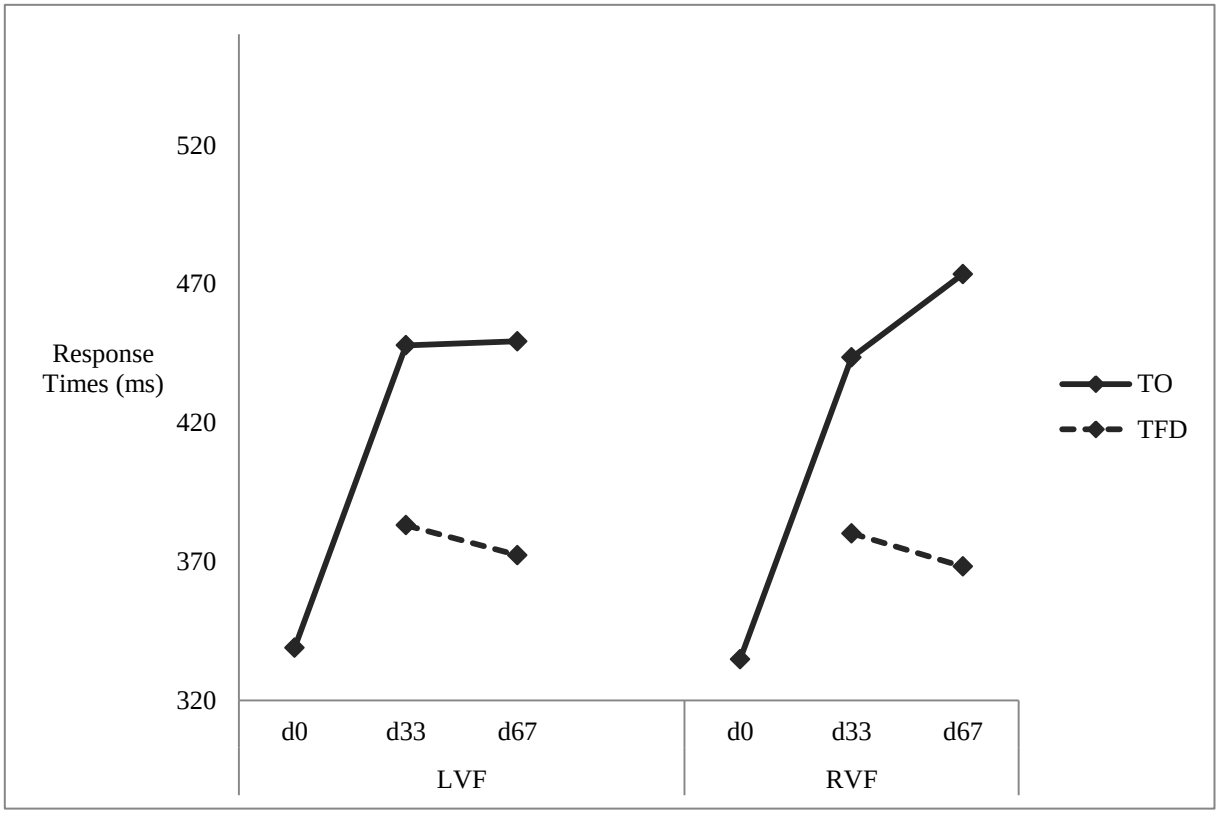

Figure 23: Mean response times in milliseconds (ms) to target-only trials (TO) and to target-following-distractor trials (TFD) in the left visual field (LVF) and in the right visual field (RVF) in Experiment 2.

There was no effect of the hand of response, $F(1, 38) < 0.01$, $p = .960$, reflecting similar global RTs for subjects responding with the left (414 ms, *SD* = 95) or the right hand (415 ms, *SD* = 86). There was a main effect of distractor percentage, $F(2, 76) = 195.98$, $p < .001$, $\eta_p^2 = .84$, indicating an increase of RTs when the percentage of distractor trials increased. As in Experiment 1, there was an interaction of Visual field x Distractor percentage, $F(2, 76) = 5.78$, $p = .005$, $\eta_p^2 = .13$. RTs increased gradually as the probability of distractors increased in the RVF (d0 = 335 ms, *SD* = 61; d33 = 444 ms, *SD* = 69; d67 = 474 ms, *SD* = 81). In the LVF, RTs increased between the blocks with and without distractors (d0 and d33), but there was a plateau between the two blocks containing distractors (d0 = 339 ms, *SD* = 55; d33 = 448 ms, *SD* = 76; d67 = 449 ms, *SD* = 81). Planned comparisons revealed that

responses in d67 were significantly slower than in d33 in the RVF, $F(1, 38) = 17.11$, $p < .001$, $\eta_p^2 = .31$, but not in the LVF, $F(1, 38) = 0.03$, $p = .865$. They also revealed no significant difference between LVF and RVF in d0, $F(1, 38) = 1.34$, $p = .255$, and in d33, $F(1, 38) = 0.30$, $p = 584$, and faster RTs in the LVF than in the RVF in d67, $F(1, 39) = 7.60$, $p = .009$, $\eta_p^2 = .17$. The analysis of the RVF data indicates that mean RTs increased linearly with the percentage of distractor trials, $F(1, 38) = 202.22$, $p < .001$, $\eta_p^2 = .84$ (The linear model explained 90% of the between-groups variance).

There was a trend towards a significant interaction Hand of response x Visual field, $F(1, 38) = 3.34$, $p = .075$, $\eta_p^2 = .08$. Planned comparisons indicated faster RTs in the LVF (407 ms, *SD* = 93) than in the RVF (421 ms, *SD* = 97) when subjects responded with their left hand, $F(1, 38) = 4.48$, $p = .041$, $\eta_p^2 = .11$, but there was not a significant difference between visual fields (LVF = 417 ms, *SD* = 84; RVF = 414 ms, *SD* = 88) when subjects responded with their right hand, $F(1, 38) = 0.22$, $p = .642$. The interaction Hand of response x Visual field x Distractor percentage was not significant, $F(2, 76) = 0.76$, $p = .470$ (see Fig. 24).

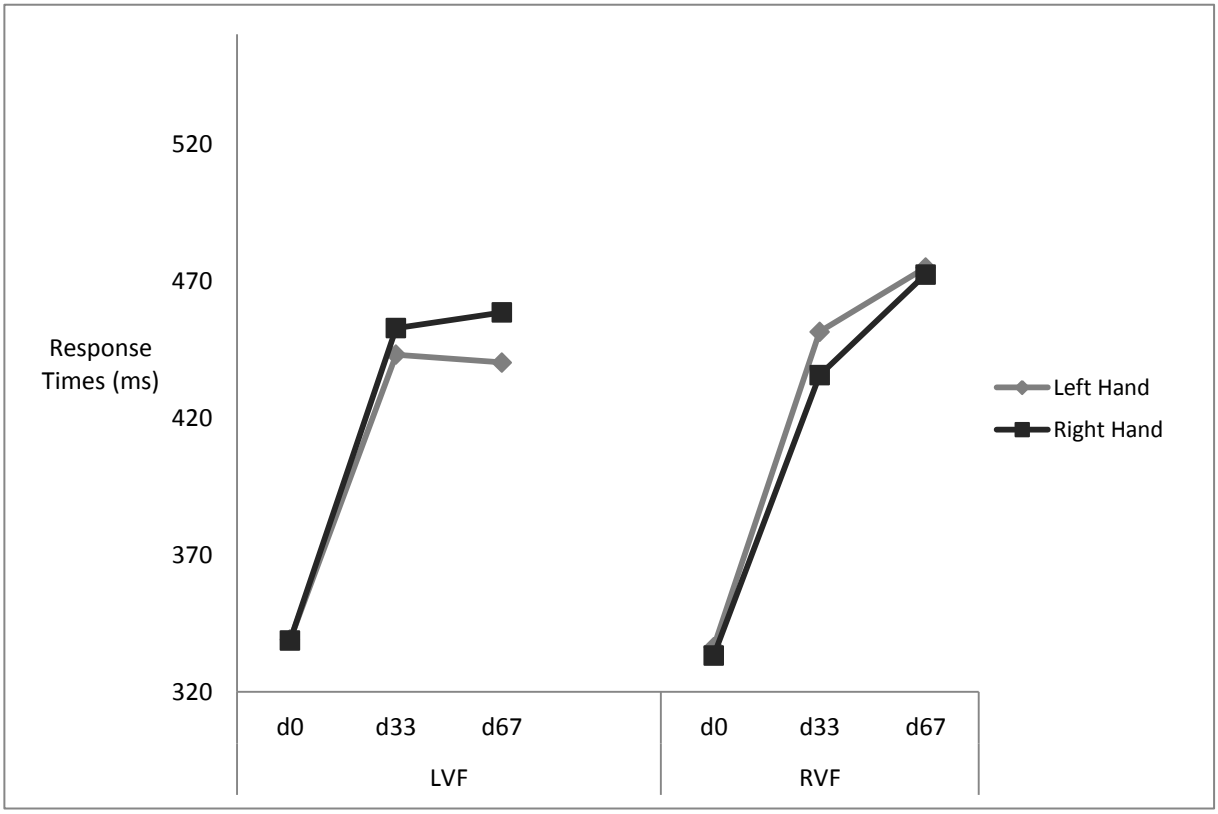

Figure 24: Mean response times in milliseconds (ms) to target-only trials as a function of hand of response (Left Hand, Right Hand) in the left visual field (LVF) and in the right visual field (RVF) in Experiment 2.

We carried out an ANOVA on the slope values with visual field (LVF, RVF) as within subjects' factor and hand of response (Left Hand, Right Hand) as between subjects' factor. The only significant main effect was visual field, $F(1, 38) = 6.03$, $p = .019$, $\eta_p^2 = .14$, indicating a smaller effect of distractor percentage in the LVF (2.0, *SD* = 0.86) than in the RVF (2.34, *SD* = 0.98).

Error data

We measured the number omissions to the target in the LVF or the RVF whichever hand was used and we computed also the false alarms by hand of response, taking into account that half of the subjects responded with the left hand and the other half with the right hand. The mean percentage of omissions was 0.90%, and the mean percentage of false alarms was 0.49 % and 0.59% for subjects responding with their right and their left hand respectively. As the frequency of errors was negligible, no further analysis was carried out with these data.

4.3.4. *Discussion*

Using a detection task, we did not obtain the RVF advantage in Experiment 2, unlike in Experiment 1. A strong possibility is that the RVF advantage found in Experiment 1 was caused by the LH implication in a task in which participants had to select a response from several alternatives (Rushworth et al., 1997; Schluter et al., 2001, 1998). Still, the results of Experiment 2 are similar to those obtained in Experiment 1, as for the global aspect of LVF and RVF RTs. Specifically, in the RVF, we obtained a gradual RTs increase as the probability of distractors increased, and, in the LVF, an increase between d0 and d33 blocks, but no difference between d33 and d67 blocks. These results are in agreement with the DH hypothesis of a differential modulation of PA by each hemisphere of the brain, namely a *frequency matching* strategy in the LH, and some *maximizing* strategy in the RH. Furthermore, using a detection task, faster RTs were found in the LVF for the block containing 67% of distractors. Consistent with RTs data, there was a smaller slope of RTs in the LVF than in the RVF, indicating less interference of the distractor for targets processed by the RH. This finding might indicate that the *maximizing* strategy developed by the RH, i.e. the enhancement of PA to the target location at longer delays, is a better strategy for behavior

optimization than the *frequency matching* strategy when there is a high temporal predictability of the target, when the percentage of distractor is high, and when the task is not controlled by the LH.

Interestingly, the pattern of results concerning the different RTs slopes in the LVF and RVF was obtained independently of the hand used to make the response. Therefore, an additional finding of Experiment 2 is that these strategies may take place at the perceptual level of processing within each hemisphere, rather than at the motor programming level. It also shows that we do not prepare in the same way to stimuli in each visual field.

4.4. General discussion

This first study aimed to examine whether PA to a spatial location in the visual field is controlled only by the RH or by both hemispheres, each hemisphere being differentially involved in the modulation of PA, especially in the case of events probability. To test the hemispheric involvement in PA, we used a lateralized version of the APT (LaBerge et al., 2000), the LAPT, in which targets were presented in RVF or LVF, thus first processed by the LH or the RH, respectively (divided visual field paradigm). Distractors were presented in the center of the display with a varying frequency for successive blocks.

A different pattern of results was found when the target appeared in the RVF or LVF. These visual field differences may be the consequence of different processing PA strategies in each hemisphere, in agreement with the DH hypothesis. In the RVF, the RTs to targets gradually increased in relation to the increase of distractors' frequency. The LH may use a *frequency matching* strategy to modulate PA, based on the actual frequency of past events (Wolford et al., 2000). Besides, RTs to targets in the LVF were affected by the mere presence or absence of distractors, but not their frequency. The RH may use a *maximizing* strategy to modulate PA, based on the processing of events with high temporal predictability. These findings are consistent with the claim that each hemisphere uses a different strategy to regulate PA to a target location.

Most importantly, our results show that these strategies are independent of the task and of the processing that takes place at the motor level. First, we obtained a similar global pattern of results with location and detection tasks, showing the differential hemispheric involvement in PA. Second, we obtained the same pattern of results whichever hand was used to make the

response in the detection task. Thus, the results of this first study suggest a differential hemispheric modulation of PA in each visual field at a perceptual level of processing.

PA in the LH

Throughout these two experiments, the RTs gradual increase in relation to the increase of distractor probability was apparent when targets were processed by the LH. This sensitivity to the frequency of events in the RVF supports the claim that the LH expectations were based on a *frequency matching* strategy (Wolford et al., 2000, 2004). We propose that the LH uses this strategy to modulate the intensities of PA directed to a spatial location. In addition to the LH sensitivity to the frequency of events, the frequency matching strategy might have been reinforced in our study by the fact that participants were acquainted with the probability of a distractor before each block of trials; therefore they were informed about the attentional demands of the upcoming block. Left areas of the prefrontal cortex were shown to have a crucial role in representing and actively maintaining the attentional demands of the task when informed in advance (MacDonald et al., 2000). The activation of these regions was related to the strategic control processes and determined by the expected level of difficulty within a task (Luks et al., 2007). In our study, shedding light with the instruction about the proportion of distractors might have reinforced the activation of the LH to develop a strategy in order to modulate PA to the target or distractor locations. It is worth noting that there was no advanced information regarding the probability of targets events (constant across trials, 50%). We may speculate that the LH might have “filled in the gap” with the missing information, “believing” that the increased probability of a distractor diminished the relative probability of a target within a block of trials. Over-interpretation, although premature and incorrect in some cases (e.g. d33, in which targets are more frequent than distractors), might also have influenced the amount of PA directed to the target location, and therefore its RTs. Such hypothesis is consistent with the claim that the LH over-interprets reality and tends to complete the pattern of missing information (Goel et al., 2007; Goel, Stollstorff, Nakic, Knutson, & Grafman, 2009).

Frequency matching may not be the most optimal strategy, especially in our experiments, where no response should be made to the distractors. Still, the LH uses this strategy, which could be some adaptation of behavior related to the ability of generating complex rules to guide behavior (Gaissmaier & Schooler, 2008; Unturbe & Corominas, 2007), searching for patterns in an uncertain world (Wolford et al., 2000, 2004). Given the

uncertainty of two events in the future (distractor and target), our results show that the LH might regulate PA directed to one event or the other according to their expected probability. This expectation might be shaped by the advance knowledge of such probabilities. In order to control for the possible effect of explicit information about the probability of distractors in the strategy develop by the hemispheres, we conducted Experiments 4 and 5 in which this information was not explicit in participants' instruction (see Chapter 6).

PA in the RH

For targets appearing in the LVF, RTs were affected by the possible occurrence of a distractor (difference between d0 and d33), but they remained constant across the two blocks containing distractors (d33, d67). In Experiments 1 and 2, targets always occurred at long delays within a trial (1800, 2000 or 2200 ms after the beginning of the trial), while distractors always occurred at shorter delays (600, 1000 or 1400 ms after the beginning of the trial). To optimize behavior, it may be that, given two events with different probabilities appearing at different delays, the RH bases expectations on the event with the highest probability of occurrence at a specific delay. More precisely, the RH strategy may rely on *maximizing* preparation to the target at longer delays owing to its high temporal predictability, and this should be the most optimal strategy. Indeed, in Experiment 2, a RTs advantage of LVF over RVF targets was found in the block containing 67% of distractors. Thus, the LVF advantage in d67 suggests that the RH strategy may be optimal to modulate PA to the target location. Consistent with this idea, a smaller slope of RTs as a function of distractor percentage was found in the LVF in Experiment 2.

Still, it can be argued that the *maximizing* RH strategy is hardly efficient, because there was a large RTs increase between d0 and d33. However, the d0 and d33 conditions are not easy to compare: there were targets and distractors in d33 while there were only targets in d0, even though participants were not informed about the total lack of distractors in this block of trials. The task is more difficult with distractors (d33) than without (d0): although participants may tend to respond systematically to the first event in the d0 block, at least after several trials when they realize that no distractor appears, they have to be more careful in the d33 block, because they might have to refrain from responding to the first event in some trials. Also, it might be very difficult to ignore distractors when they are centrally presented, especially when targets are presented in two peripheral locations (Beck & Lavie, 2005).

Altogether, the results for targets appearing in the LVF suggest that the intensity of PA directed to the target location by the RH was only influenced by the presence of a distractor within a block of trials and not by the probability of distractor occurrence. It might also be suggested that the intensity of PA directed by the RH is influenced by the temporal predictability of the target. To explore further the role of the target temporal predictability in the hemispheric modulation of PA, we designed Experiment 3 (Chapter 5), in which the target can appear at various delays, short and long, within a trial, therefore rendering a *maximizing* strategy more difficult to achieve.

Hemispheric preparatory strategies and the triangular circuit theory of attention

The strategies developed by each hemisphere might presumably be generated in prefrontal areas of selective control that determines whether attention is directed to the target or distractor site of attentional expression (see Fig. 25) (LaBerge et al., 2000). The selective control activates the distractors and targets sites in the modulatory control. The modulatory control determines how intense the activity will be in cortical areas of attentional expression, in relation to expectations (strategy). Also, expectations might depend on the parietal lobe (LaBerge & Brown, 1989). The modulatory control information is send to the thalamus that enhances activity to one or the other site in areas of attentional expression. Therefore, the sensory information arising from each visual field is modulated by the attentional bias towards targets and/or distractors already present in brain areas of attentional expression. This bias is related to the strategy generated by the selective control of attention in each brain hemisphere.

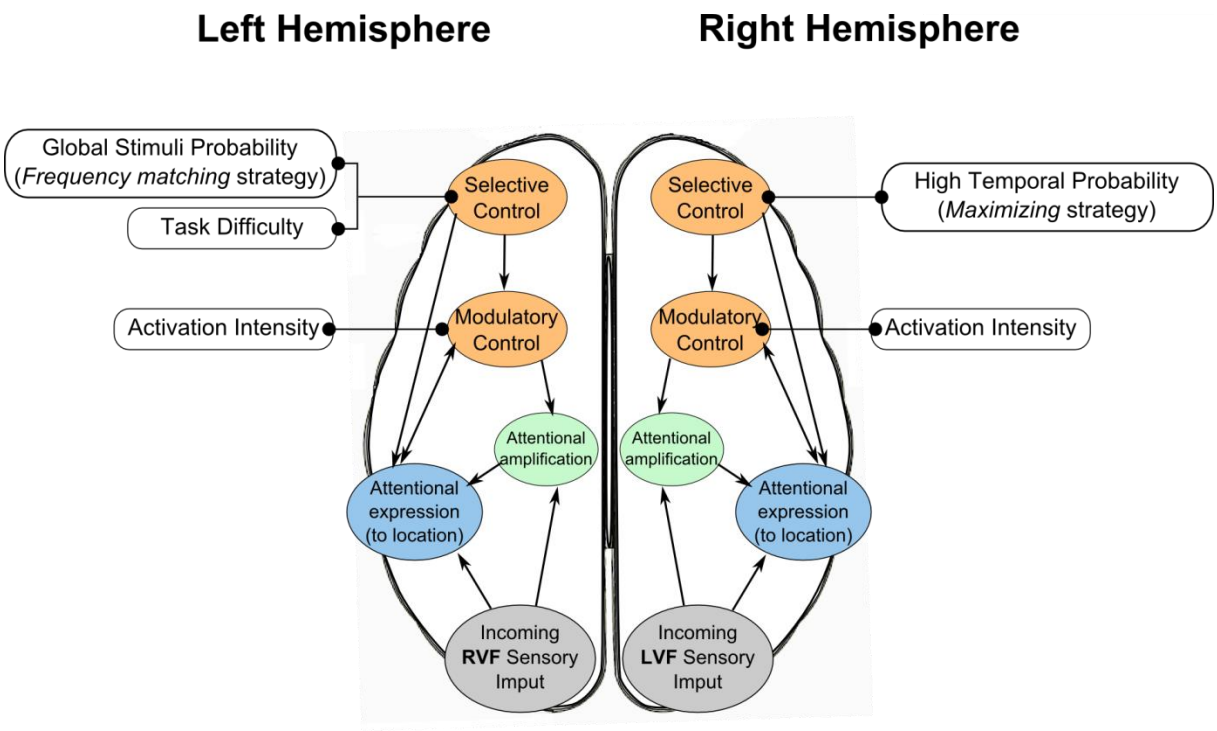

Figure 25: Schematic illustration of the modulation of PA by the thalamocortical circuit in each hemisphere when the temporal predictability of a target stimulus within a trial is high and the proportion of distractors are explicitly informed.

4.5. Conclusion

The findings of this first study using the LAPT suggest that the modulation of PA to a spatial location differs in the LVF and the RVF, and that this modulation is related to the processing of events probability. As RVF and LVF stimuli are first processed by the LH or the RH respectively, these visual field effects can reflect hemispheric differences in PA. Each hemisphere may use a different strategy to modulate PA to a visual location at the perceptual level of processing. PA in the LH might be modulated by the expected probability of targets and distractors, taking into account their frequency in the past. We explore the modulation of PA in the RH in the next experimental study.

CHAPTER 5 - Effect of temporal probability of stimuli on the hemispheric modulation of PA

5.1. Presentation of the study

In our world, space and time are two dimensions in constant interaction. The amount of PA directed to a spatial location before a stimulus appearance is also influenced by the specific delay at which that stimulus is expected. Several studies suggest that the direction of attention on a specific time interval benefits to the processing of a target stimulus appearing within that interval (Coull et al., 2000). When targets can occur at different time intervals within a trial, responses are faster at the interval in which the target has the highest probability of occurrence (Niemi & Näätänen, 1981; Trillenberg et al., 2000). This behavioral benefit has been related to the strategic enhancement of attentional activity at the interval in which the target is highly predictable. Thus, stimuli temporal probability might have a particular role in the strategic regulation of PA. The aim of this second study was to investigate the influence of the temporal probability of a target stimulus on the modulation of PA by each hemisphere.

The temporal probability of a target stimulus may influence the expectations concerning that stimulus using RH mechanisms. The RH is specifically involved when processing target stimuli with high regularity and temporal probability, thus highly predictable events. Frontal areas of the RH were particularly involved in the voluntary enhancement of attention at time intervals at which the target is highly predictable (Coull et al., 2000; Vallesi et al., 2008). The findings of our previous study (Chapter 4) might also be in agreement with a role of the RH in modulating PA according to the high temporal predictability of a target stimulus within a trial. In Experiments 1 and 2, targets and distractors never appeared together within a trial: there was a variable time interval in which a distractor could appear followed by a variable time interval in which the target could appear, named short and long delays, respectively. The RH may have maximized the enhancement of PA at long delays within a trial (no difference between d33 and d67 blocks, varying the percentage of distractors), given the high temporal predictability of a target occurrence at those delays. Thus, it can be argued that the temporal predictability or certainty of a target stimulus has a crucial role for the RH modulation of PA.

The results obtained in our previous study suggest that the LH might differ from the RH in the strategy used to regulate the intensity of PA towards a stimulus location. We proposed that the LH used a *frequency matching* strategy to modulate PA, taking into account the probability of targets and distractors within a block of trials. The LH may distribute preparatory attentional resources to one or the other stimuli according to their expected probability. A possibility is that the strategy developed by the LH is related to the global expected probability of targets and distractors in a block of trials, but not to the delay in which they are expected to occur. The temporal predictability of a target stimulus might not particularly influence the modulation of PA in the LH.

In this second study we tested the influence of the temporal probability of the target on the preparatory strategy developed by each hemisphere. We designed Experiment 3, in which the temporal probability of events was manipulated. Like in Experiments 1 and 2, the probability of distractors increased along three consecutive blocks of trials (d0, d33, and d67). However, the probability of the delay at which a target could appear within a trial was different, influencing its temporal predictability. In Experiment 3, the target might appear at short or long delays within a trial, having a low temporal predictability. Like in previous experiments, the distractor appeared only at short delays within a trial. This means that even though targets and distractors never appeared simultaneously (like in Experiment 1 and 2) the delay at which distractors can appear overlaps with one of the delays in which a target might occur (unlike in Experiments 1 and 2). Thus, a strategy of expecting a target stimulus, and only the target stimulus, at a specific interval within a trial is less suitable for the constraints of this experiment.

If the RH strategy in modulating PA to an expected target stimulus is related to its high temporal predictability within a trial, it should be affected by a manipulation of the delay at which that target can appear. More precisely, the lower predictability of the target within a trial in Experiment 3 should prevent the RH strategy of maximizing PA. Besides, if the LH preparatory strategy is related to the expected stimuli frequency and not to the expected delay of their appearance, the manipulation of stimuli delay should not particularly influence the *frequency matching* strategy in the RVF. This means that RTs in the RVF should increase as a function of the probability of distractors, regardless of stimuli temporal uncertainty, like in previous experiment. A strong possibility is that this strategy would also apply to the whole visual field, including LVF, because it is not “counterbalanced” by a RH maximizing strategy.

Experiment 3

In Experiment 1 and 2, RTs to the LVF target remained constant across the two blocks containing distractors, d33 and d67, although the RTs increased in the RVF as the probability of distractors increased. A possibility is that the RH somewhat maximizes the enhancement of PA at long delays within a trial, given the target predictability at these delays, and the LH matches PA to the frequency of targets in relation to distractors. Experiment 3 was designed to explore further these hemispheric strategies in a condition in which the target temporal predictability within a trial was lower. The target could appear at short delays, like distractors, or at long delays. Whereas the RH *maximizing* strategy, i.e. similar RTs for d67 and d33, should be affected by the target temporal probability manipulation, the LH *frequency matching* strategy should not.

5.2. Methods

Participants. Forty students (14 men and 26 women) of the Institut de Psychologie at Paris Descartes University (M_{age} = 20.3 years, *SD* = 1.6; age range: 18-26 years), different from Experiment 1 and 2, participated in Experiment 3. They had normal or corrected-to-normal vision and no psychiatric or neurological history, learning disability or attentional deficit, as assessed by self-report. They were all right-handed (*M* = 87), as evaluated with the Edinburgh Handedness Inventory (Oldfield, 1971). All participants provided informed consent and received course credits for participating in the experiment.

Stimuli. Stimuli were the same as in Experiment 1 and 2.

Procedure. Experiment 3 was the same to Experiment 1 with the following exceptions. When the target appeared alone within a trial (TO trials), it could appear 50 % of the times 600, 1000 or 1400 ms (short delay) after the warning signal, thus at the same delays as the distractor, and, the other 50% of the times, 1800, 2000 or 2200 ms (long delay) after the warning signal presentation. Note that the target always appeared at a long delay when preceded by a distractor (TFD trials) (see Table 3). As in Experiment 1, the task was a location task.

Table 3

Frequencies of trial types within a block of trials for each SOA (Short, Long) in each visual field (LVF, RVF)

		Percentage of distractor trials					
		0		33		67	
Trial type	SOA	LVF	RVF	LVF	RVF	LVF	RVF
Blank	Short	36		24		12	
	Long						
Target-only	Short	9	9	6	6	3	3
	Long	9	9	6	6	3	3
Target-following-distractor	Short	0		0	0	0	0
	Long			6	6	12	12
Distractor-only	Short	0		12		24	
	Long			0		0	

5.3. Results

Mean RTs on TO and TFD trials are shown in Figure 26. See Table 4 for the complete RTs data.

Table 4

Mean response times in milliseconds and standard deviations (in parentheses) in Experiment 3 for target-only trials (TO) and target-following-distractor trials (TFD), as a function of the delay of appearance (short, long) and the visual field (LVF, RVF) in each block of trials (d0, d33, d67).

Experiment number			TO			TFD	
	SOA	VF	d0	d33	d67	d33	d67
Experiment 3	Short	LVF	378 (53)	457 (63)	477 (101)		
		RVF	377 (52)	441 (49)	467 (84)		
	Long	LVF	370 (55)	439 (60)	461 (100)	401 (70)	388 (79)
		RVF	366 (55)	434 (68)	445 (89)	391 (64)	381 (61)

TO trials

A repeated measures ANOVA was calculated on mean RTs in TO trials, with distractor percentage (d0, d33, d67), visual field (LVF, RVF), and SOA (short, long) as within subjects' factors.

There was an effect of distractor percentage, $F(2, 78) = 111.84$, $p < .001$, $\eta_p^2 = .74$, indicating an increase of response times when the percentage of distractor trials increased. There was a significant main effect of visual field, $F(1, 39) = 4.36$, $p = .043$, $\eta_p^2 = .10$, with faster RTs in the RVF (422 ms, *SD* = 77) than in the LVF (430 ms, *SD* = 85). There was also a main effect of SOA, $F(1, 39) = 12.45$, $p = .001$, $\eta_p^2 = .24$, reflecting faster RTs when the target appeared at long delays (419 ms, *SD* = 81) than short delays (433 ms, *SD* = 80). No interaction between factors reached significance, specifically the interaction Distractor percentage x Visual field, $F(2, 78) = 0.80$, p = .454. Planned comparisons were calculated in order to examine the effects of distractor percentage within each visual field because these effects were of theoretical interest. The comparisons revealed that RTs were significantly slower in d67 than in the d33 in the RVF, $F(1, 39) = 5.74$, $p = .021$, $\eta_p^2 = .13$, as well as in the LVF, $F(1, 39) = 5.17$, $p = .029$, $\eta_p^2 = .12$.

We carried out an ANOVA on the slope values with visual field (LVF, RVF) and SOA (short, long) as within subjects' factor. There was a slightly larger slope of RTs in the LVF (1.59, *SD* = 0.94) than in the RVF (1.49, *SD* = 0.95), but this difference was not significant, $F(1, 39) = 2.14$, $p = .152$. There was also a slightly larger slope for shorter SOA (1.58, *SD* = 0.87) than for longer SOA (1.44, *SD* = 0.97), but this difference did not reach significance, $F(1, 39) = 1.14$, $p = .292$. No interaction between factors reached significance.

TFD trials

A repeated measures ANOVA was calculated on mean RTs in TFD trials, with distractor percentage (d33, d67) and visual field (LVF, RVF) as within subjects' factors. The slight difference between the RVF (386 ms, *SD* = 62) and the LVF (394 ms, *SD* = 75) was not significant, $F(1, 39) = 3.26$, $p = .079$. There was a trend towards faster RTs in d67 (384 ms, *SD* = 70) than in d33 (396 ms, *SD* = 67), $F(1, 39) = 3.81$, $p = .058$, $\eta_p^2 = .09$. No other main effect or interaction between factors reached significance.

Error data

We measured the number of omissions and false alarms. The mean percentage of omissions was 0.19%, and the mean percentage of false alarms was 0.28 %. As the frequency of errors was negligible, no further analysis was carried out with these data.

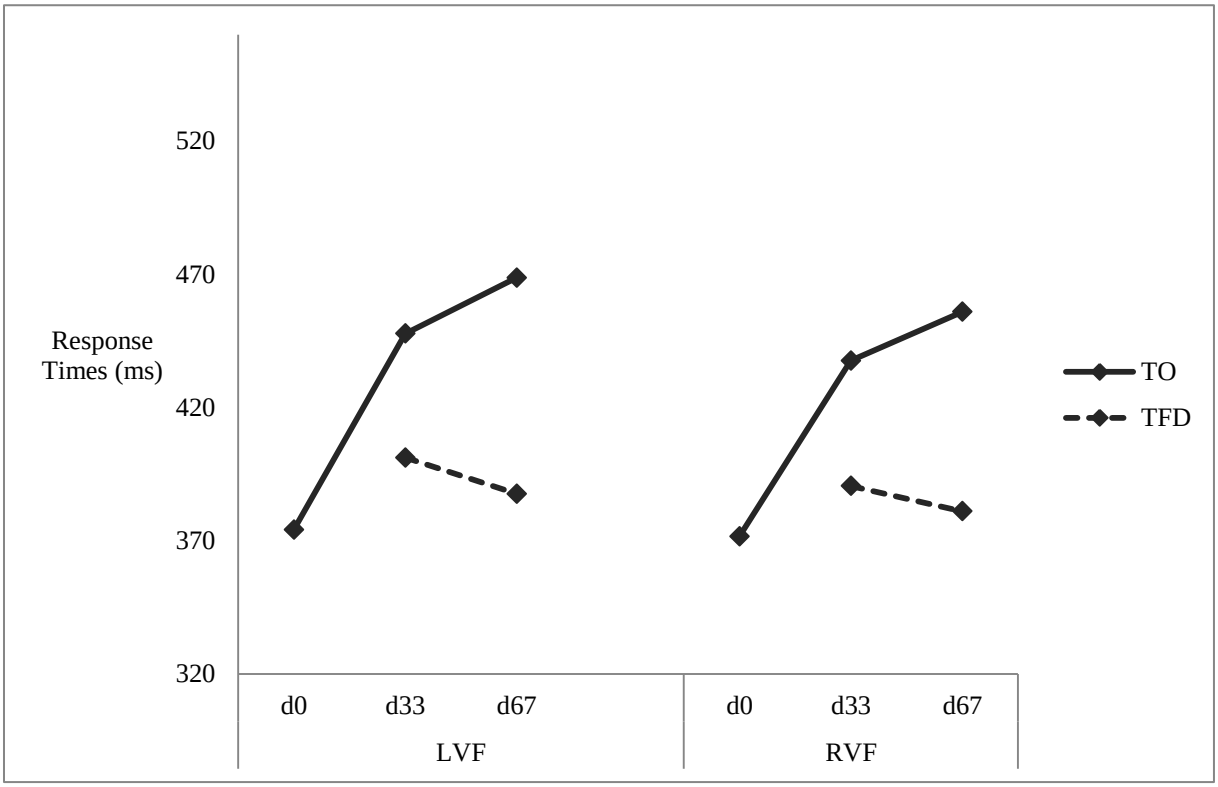

Figure 26: Mean response times in milliseconds (ms) to target-only trials (TO) and to target-following-distractor trials (TFD) in the left visual field (LVF) and in the right visual field (RVF) in Experiment 3.

5.4. Discussion

The aim of this second study was to examine the influence of stimuli temporal probability in the modulation of PA by each hemisphere. We found a main effect of distractor percentage in TO trials indicating an augmentation of RTs as the probability of distractors increased, like in Experiments 1 and 2. However and most importantly, this increase of RTs was found with RVF targets, as in Experiment 1 and 2, but also with LVF targets, unlike Experiments 1 and 2. We were particularly interested in the comparison of RTs between d33 and d67 in the LVF. Although no difference occurred in the experiments presented in Chapter 4, RTs were significantly longer in d67 compared to d33 in Experiment 3. These results somewhat enlighten the role of the RH in PA. The RH may have developed some *maximizing* strategy in Experiments 1 and 2, but not in Experiment 3, when the target's delay was less

predictable. This result is in agreement with the idea that the temporal probability of the target affected the modulatory strategy of PA in the RH but not necessarily in the LH.

We also obtained an effect of SOA indicating that RTs to targets appearing at long delays were faster than to targets appearing at short delays. A first possibility is that PA takes time to develop (Jennings & van der Molen, 2005), favoring responses to targets occurring at the long delay. A second possibility is that PA is reinforced by the higher conditional probability of the target occurrence as time passes within a trial. Several studies have shown that responses to stimuli are faster as time passes when there is time uncertainty (for a review, see Niemi & Näätänen, 1981), and the RH might be specifically involved in this phenomenon (Vallesi et al., 2008). Faster responses to target occurring at the long delay in our experiment may be caused by the RH strategy facing the higher conditional probability of the targets at this delay. However, we found faster RTs for targets with long delays independently of the visual field of presentation. Also, it might have been difficult in our experiment to develop this specific strategy of reinforcing PA by the higher conditional probability within a trial, because targets occurred only in 50% of the trials, and long delay targets in TO trials were rare in d33 (16.7%) and d67 (8.3%). Thus, the explanation of the effect of SOA might well be the time necessary to develop PA rather than a difference in the conditional predictability of the target occurrence. The time necessary to develop PA may not be lateralized.

We found a main effect of visual field with faster RTs to targets in the RVF than in the LVF, showing an advantage of the LH. Interestingly, in Experiment 1, we also obtained faster RTs in the RVF for TO trials in the block containing 33% of distractors. This hemispheric advantage might be due to the location task used in Experiments 1 and 3, as the LH was shown to be particularly involved in complex tasks with several response alternatives (Rushworth et al., 1997; Shluter et al., 1998, 2001). Consistent with this proposal, there was no visual field advantage in a less demanding task (Experiment 2). Another possibility that might contribute to the RVF advantage is the specific recruitment of the LH in Experiment 3 owing to the uncertain context in which stimuli are presented.

LH preparatory strategy in both visual fields

It is interesting to ascertain that the LVF pattern of responses in Experiment 3 is very similar to the RVF pattern of responses in Experiments 1-3. The RH may not maximize the enhancement of PA to the LVF target in Experiment 3 given the temporal uncertainty of the

target within a trial. The difficulty of the RH to develop its strategy may reinforce the relative control of the LH in PA. The reinforcement of the LH activation may result in a *frequency matching* strategy applied to the whole visual field. However, the research in the spatial attentional domain mostly shows that the LH is able to allocate attention only to the RVF while the RH is able to allocate attention to the whole visual field (Corbetta, Miezin, Shulman, & Petersen, 1993; Heilman & Valenstein, 1979; Mesulam, 1981; Perry & Zeki, 2000). How these findings can be reconciled with the proposal that the strategy developed by the LH applied not only to the RVF but also to the LVF in specific situations?

A possibility is that modulation of PA interacts between hemispheres. According to the model of LaBerge et al. (2000), the modulatory control receives information generated in the selective control, both located in frontal areas. The modulatory control of the LH may receive information generated in the ipsilateral selective control areas, and transfer information, presumably by the corpus callosum, to the modulatory control area located in the RH (see Fig. 27). Consequently, the intensification of activity in targets and distractors sites in posterior areas of the RH is influenced by the attentional bias towards targets and distractors generated by the LH. The processing of sensory information arising from LVF input is thus modulated by the strategy developed in prefrontal areas of the LH, giving as a consequence a similar pattern of responses in both visual fields. As information transfer between hemispheres is time consuming (Iacoboni & Zaidel, 2000; Marzi, Bisiacchi, & Nicoletti, 1991; Weber et al., 2005), RTs in the LVF are slower than in the RVF. In the latter case (RVF targets), the control (selective and modulatory), mechanism, and expression areas of attention are part of the same hemisphere.

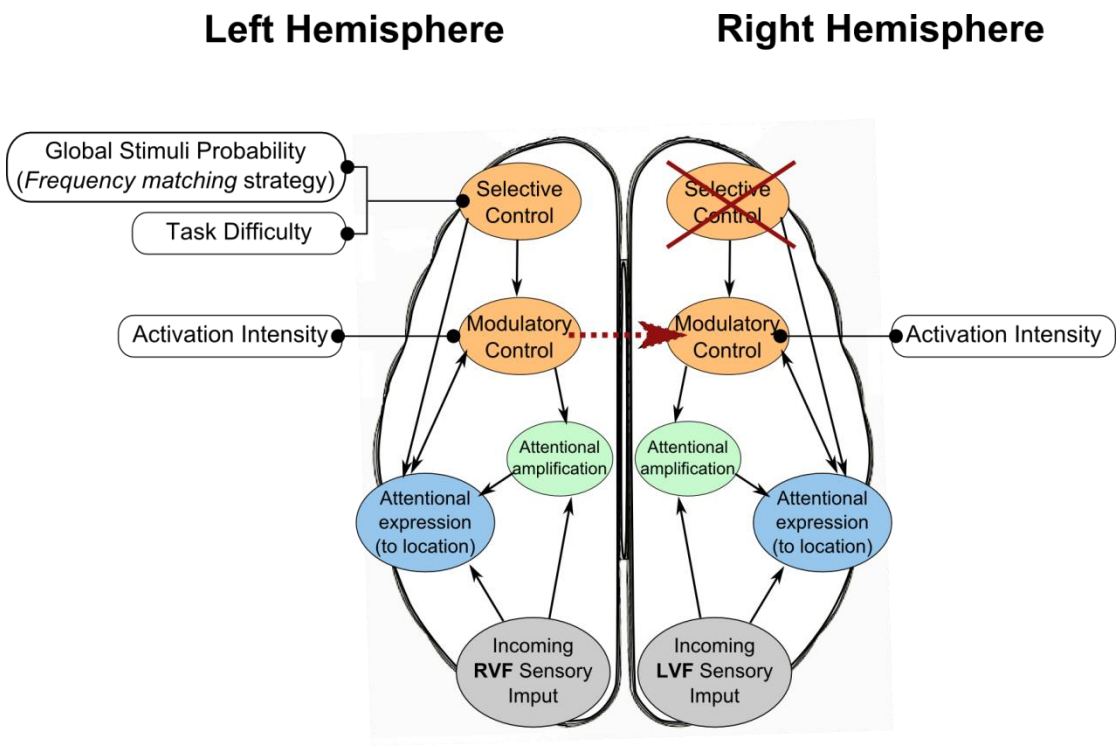

Figure 27: Schematic illustration of the modulation of PA by the thalamocortical circuit in each hemisphere under stimuli temporal uncertainty.

RVF advantage and the role of the LH under stimuli uncertainty

In Experiment 3, the temporal interval at which the target can appear was harder to discriminate from the temporal interval in which a distractor was expected, making the temporal allocation of PA resources more difficult. It might be speculated that, in Experiment 3, the task was perceived as more difficult to perform because of the temporal uncertainty of the target, which might increase the attentional demands required to respond correctly. Thus, the temporal uncertainty of events might have reinforced the LH activation to develop a preparatory strategy, given the perceived difficulty to discriminate the temporal interval in which relevant and irrelevant information are expected. This proposal is in agreement with studies showing that the LH is particularly recruited to develop a preparatory strategy in difficult situations (Luks et al., 2007; MacDonald et al., 2000) when more attentional control is needed to select relevant information.

5.5. Conclusion

The findings of this second study suggest that the RH modulation of PA to a target location is sensitive to the temporal probability of the target. The temporal uncertainty of the target might prevent the RH to maximize the enhancement of PA in the LVF. The uncertainty context in which stimuli appear as well as the RH difficulty to develop a preparatory strategy may reinforce the relative control of the LH in PA. The reinforcement of the LH activation may result in a *frequency matching* strategy applied to the whole visual field. The LH attentional control might modulate the activity of posterior areas of attentional expression through an inter-hemispheric neural pathway. Hence, the findings of the present study suggest that stimuli temporal probability has a role in the preparatory strategies developed by each hemisphere and open a possible distinction of intra- *vs* inter-hemispheric pathways in the triangular circuit of attention.

CHAPTER 6: Implicit learning of stimuli probability and the modulation of PA

6.1. General presentation of the study

The amount of attentional activity directed to a stimulus prior to its occurrence is modulated by its expected probability. The probability of a stimulus can be explicitly informed in advance or can be implicitly learned from the sequence of events. In the experimental studies presented in previous Chapters, subjects were explicitly informed about the proportion of distractors before each block of trials. The goal of this third study was to examine the modulation of PA by each hemisphere when the increasing probability of distractors was learned from the sequence of trials.

The results of our previous studies showed a different pattern of responses in the RVF/LH and the LVF/RH. The responses to RVF/LH targets exhibited a *frequency matching* pattern. This pattern of responses was associated with the LH sensitivity to the frequency of events, although it is not yet clear whether the effect of events frequency in the RVF/LH is the consequence of an automatic or controlled process. A first hypothesis is that the LH may automatically record the frequency of events (Lamb et al., 1998; Risko et al., 2008). In that case, the *frequency matching* observed in previous experiments would be the result of the automatic computation of frequencies throughout the sequence of trials. A second hypothesis is that *frequency matching* relies on strategic and controlled processes. The LH may strategically distribute PA to stimuli according to their expected probability. In Experiments 1-3, the proportion of distractors was explicitly informed in advance. The anticipation of the proportion of distractors might presumably allow the LH to prepare strategically to the upcoming events. In that case, the explicit instruction in previous experiments may have been crucial for the LH development of a *frequency matching* strategy to distribute attentional resources prior to events occurrence (Luks et al., 2007; MacDonald et al., 2000).

LVF/RH targets exhibited a different pattern of responses depending on the temporal predictability of the target. When the target had a high temporal predictability within a trial (Experiments 1 and 2), responses showed a sort of *maximizing* pattern. *Maximizing* has been

traditionally associated with the most optimal strategy when the presentation of events with different probabilities is randomized (Estes, 1976; Hinson & Staddon, 1983). In the frame of probability guessing tasks, Fantino and Estefarandi (2002) demonstrated that subjects tended to use a more optimal strategy when explicitly informed about the probability of events. In other words, the anticipation of events probability might reinforce the development of a *maximizing* strategy. It can be argued that in our previous experiments the explicit information about the proportion of distractors reinforced the *maximizing* strategy in the RH when events had a high temporal predictability. Therefore, the information about the probability of distractors might have modulated the deployment of a preparatory strategy in both hemispheres.

We designed Experiments 4 and 5 to explore the modulation of PA in each hemisphere when no specific information is given about the probability of distractors. Precisely, in this third study we tested the influence of distractor probability on the intensity of PA directed to a target location when this probability is learned from the sequence of trials. The probability of distractors increased along three consecutive blocks, like Experiments 1-3. However, participants were not explicitly informed about the proportion of distractors before the beginning of each block (hereafter *D-implicit* instruction). Rather, in the present study participants had to get acquainted from the sequence of trials (including the 12 "practice" trials in the beginning of each block) with the differential proportion of distractors between blocks. The target had a high temporal predictability within a trial, as in Experiments 1 and 2, meaning that when a target occurred it always occurred at long delays.

The results of our previous experiments suggested that both hemispheres were equally involved in a simple detection task (Experiment 2). Therefore, we used a detection task in Experiment 4 because this task should allow a better evaluation of the modulation of PA with a *D-implicit* instruction. Additionally, our previous results suggested that the LH was especially implicated in more complex tasks with several response alternatives (location task in Experiments 1 and 3). However, the role of the task in the LH pattern of results remains to be clarified. Thus, an additional goal in the present study was to examine the role of a complex task for the LH. It might be possible that the complexity of the task *per se* activates the LH to develop a preparatory strategy. We used a location task in Experiment 5 to test this possibility.

With this paradigm, we examined the modulation of PA in each visual field/ hemisphere under implicit learning of stimuli probability. If the *frequency matching* found in

the RVF in previous experiments is related to an automatic computation of frequencies in the LH, we should obtain a similar pattern of responses to Experiments 1-3 for RVF targets, whichever the task. The RTs to the target should increase as a function of the probability of distractors (*frequency matching*). In contrast, if the *frequency-matching* pattern of results is associated to the LH ability to strategically control the distribution of attentional resources according to expected probabilities, this strategy might be affected by the lack of explicit information about the increasing proportion of distractors before each block of trials. Additionally, if the preparatory strategy in the LH can be trigged by the complexity of the task, we should obtained a *frequency matching* pattern of responses in the RVF with the location task (Experiment 5) but not with the detection task (Experiment 4). Besides, if the explicit information about distractor probability reinforces the RH *maximizing* strategy, this strategy should be affected when using a *D-implicit* instruction, whichever the task.

6.2. Experiment 4

6.2.1. *Presentation of the experiment*

In this experiment, we examined the modulation of PA in both hemispheres when the proportion of distractors has to be learned from the sequence of trials. The distractor probability varied in three blocks of trials (absent, rare, frequent) but there was a lack of explicit information about this variation (*D-implicit* instruction). The target had a high temporal predictability within a trial. We used a detection task, i.e. only one possible response, in order to reduce the LH control over the task. The detection task should allow a better evaluation of each hemisphere strategy with a *D-implicit* instruction.

6.2.2. *Methods*

Participants. Forty students (12 men and 28 women) of the Institut de Psychologie at Paris Descartes University (M_{age} = 22.1 years; *SD* = 3.9; age range: 18-36 years), different from Experiments 1-3, participated in Experiment 4. They had normal or corrected-to-normal vision and no psychiatric or neurological history, learning disability or attentional deficit, assessed by self-report. They were all right-handed (*M* = 83), evaluated with the Edinburgh

Handedness Inventory (Oldfield, 1971). All participants provided informed consent and received course credits for participating in the experiment.

Stimuli. Stimuli were the same as in Experiment 1-3.

Procedure. Experiment 4 was the same to Experiment 2 with the exception of the instruction given to participants. In Experiment 4 participants were not explicitly informed before each block of trials about the proportion of a distractor appearance (*D-implicit* instruction).

6.2.3. *Results*

Mean RTs on TO and on TFD trials are shown in Figure 28. See Table 5 for the complete RTs data.

Table 5

Mean response times in milliseconds and standard deviations (in parentheses) for target-only trials (TO) and target-following-distractor trials (TFD) of Experiments 4 and 5, for each visual field (LVF, RVF) in d0, d33, and d67.

Experiment number	VF	TO			TFD	
		d0	d33	d67	d33	d67
Experiment 4	LVF	338 (78)	420 (79)	420 (82)	357 (83)	360 (86)
	RVF	330 (63)	404 (66)	416 (84)	355 (74)	344 (77)
Experiment 5	LVF	357 (61)	457 (68)	451 (80)	384 (64)	365 (68)
	RVF	348 (54)	454 (76)	447 (84)	384 (78)	367 (69)

TO trials

A repeated measures ANOVA was calculated on mean RTs, with hand of response (left hand, right hand) as between subjects' factor, and distractor percentage (d0, d33, d67) and visual field (LVF, RVF) as within subjects' factors.

There was no effect of the hand of response, $F(1, 38) = 0.66$, $p = .422$, reflecting similar global RTs for subjects responding with the left (427 ms, $SD = 93$) or the right hand (411 ms, $SD = 75$). The factor hand of response did not interact with any other factor. There

was a main effect of distractor percentage, $F(2, 76) = 150.37$, $p < .001$, $\eta_p^2 = .80$, indicating an increase of RTs when the percentage of distractor trials increased. The interaction Distractor percentage x Visual field was not significant, $F(2, 76) = 0.26$, $p = .770$. However, planned comparisons were performed in order to examine the effects of distractor percentage within each visual field since these effects were of theoretical interest. The comparisons revealed that there was no significant difference between the RTs in d67 and the d33, either in the RVF, $F(1, 38) = 0.62$, $p = .437$, or the LVF, $F(1, 38) = 0.52$, $p = .475$. Planned comparisons also indicate faster RTs in the RVF than the LVF in d0, $F(1, 38) = 6.10$, $p = .018$, $\eta_p^2 = .14$, and no significant difference in d33, $F(1, 38) = 0.13$, $p = .725$, or d67, $F(1, 38) = 0.12$, $p = .735$.

We carried out an ANOVA on the slope values with visual field (LVF, RVF) as within subjects' factor and hand of response (left hand, right hand) as between subjects' factor. The difference between the slope in the LVF (1.73, *SD* = 0.88) and the RVF (1.85, *SD* = 0.90) was not significant, $F(1, 38) = 0.66$, $p = .421$. No other main effect or interaction reached significance.

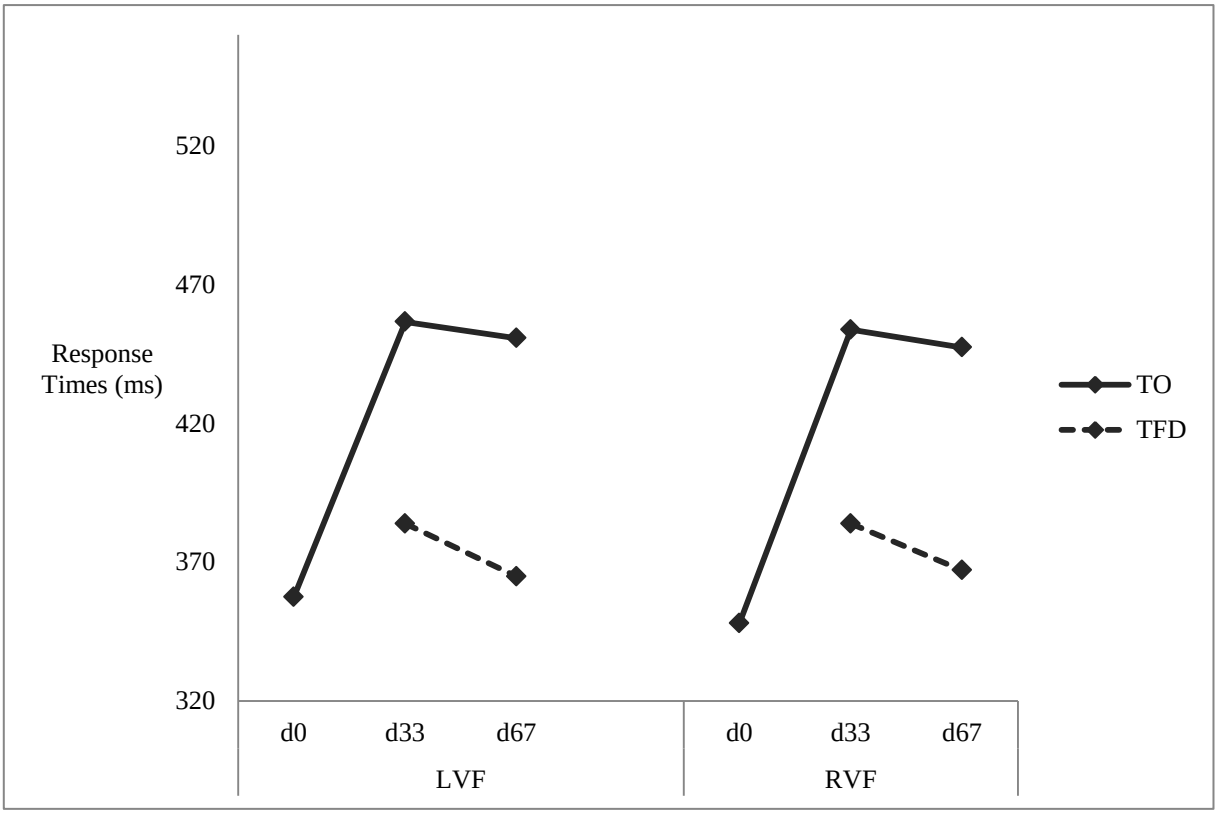

Figure 28: Mean response times in milliseconds (ms) to target-only trials (TO) and to target-following-distractor trials (TFD) in the left visual field (LVF) and in the right visual field (RVF) in Experiment 5.

TFD trials

A repeated measures ANOVA was calculated on mean RTs, with hand of response (left hand, right hand) as between subjects' factor, and with distractor percentage (d33, d67) and visual field (LVF, RVF) as within subjects' factors.

The difference between the RVF (375 ms, *SD* = 73) and the LVF (374 ms, *SD* = 66) was not significant, $F(1, 38) = 0.1$, $p = .756$. There was a significant main effect of distractor percentage, $F(1, 38) = 7.36$, $p = .01$, $\eta_p^2 = .16$, with faster RTs in d67 (366 ms, *SD* = 68) than in d33 (384 ms, *SD* = 71). The only significant interaction was Visual field x Hand, $F(1, 38) = 12.39$, $p = .001$, $\eta_p^2 = .25$. This interaction was due to faster RTs in the LVF (383 ms, *SD* = 68) than in the RVF (397 ms, *SD* = 71) when participants responded with their left hand, $F(1, 38) = 7.35$, $p = .01$, $\eta_p^2 = .16$, and faster RTs in the RVF (354 ms, *SD* = 70) than in the LVF (366 ms, *SD* = 64) when participants responded with their right hand ,$F(1, 38) = 5.14$, $p = .029$, $\eta_p^2 = .12$. No other main effect or interaction between factors reached significance.

Error data

We measured the number omissions to the target in the LVF or the RVF whichever hand was used and we computed also the false alarms by hand of response, taking into account that half of the subjects responded with the left hand and the other half with the right hand. The mean percentage of omissions was 0.83%, and the mean percentage of false alarms was 0.61 % and 0.46% for subjects responding with their right and their left hand respectively. As the frequency of errors was negligible, no further analysis was carried out with these data.

6.2.4. *Discussion*

The main finding of Experiment 4 is that the pattern of responses for TO trials changed when the proportion of distractors had to be learned from the sequence of trials compared to the condition in which the proportion of distractors was explicitly informed before each block. Interestingly, the absence of explicit information about the increasing proportion of distractors across blocks modified the pattern of results only for RVF targets, processed by the LH.

For RVF targets, RTs increased between the blocks with and without distractors (d0 and d33), but there was a lack of difference between the two blocks containing distractors. The lack of explicit information about the increasing proportion of distractors in Experiment 4 seemed to prevent the LH to develop a *frequency matching* strategy. This result suggests that the *frequency matching* in the RVF is mostly associated with controlled processes, rather than with the automatic computation of events' frequency. Still, it is possible that the LH kept the record of events frequency, but this information was not strategically used to control the allocation of attention presumably because of the task short duration. The LH may need more time to implicitly learn the probability of targets and distractors and develop a preparatory strategy based on these probabilities. Additionally, the relatively low demands of resources associated with the detection task may also reduce the LH recruitment to develop a preparatory strategy. The question is whether a more complex task *per se* can trigger a *frequency matching* strategy. This question is addressed in Experiment 5.

For LVF targets, processed by the RH, the pattern of responses was similar to those obtained in previous experiments (Experiments 1 and 2), using a high temporal predictability of targets, like this experiment, and an explicit instruction on the distractor probability, unlike this experiment. This finding shows that the RH preparatory strategy was not affected by the instruction. The RH may implicitly learn the timing of events from the sequence of trials and the knowledge about distractors proportion may not affect this learning process. Thus, this finding strengthens the idea that the RH *maximizing* strategy is associated with the temporal probability or certainty of the target event, presumably learned from the sequence of trials.

In trials in which the target appeared after a distractor (TFD), RTs to the target were faster when the response was executed with the hand ipsilateral to the visual field of presentation. Precisely, RTs were faster in the RVF when responses were executed with the right hand, and in the LVF when responses were executed with the left hand. This stimulus-response compatibility effect can be associated to an automatic facilitation of the response processing in the same hemisphere receiving the perceptual input (e.g. De Jong, Liang, & Lauber, 1994). There was also an effect of distractor probability for TFD trials indicating faster RTs in d67 than in d33. The increased proportion of trials in which a distractor preceded a target in d67 might increase the cuing force of the distractor, increasing the attention directed to the target location after the distractor occurrence. As a consequence, RTs to TFD trials decreased as the probability of distractors increased. It is worth noting that there was a difference between d67 and d33 in TFD trials while in TO trials there was not such a

difference. Also, the hand of response correlated with visual field differences in TFD trials, while in TO trials the pattern of responses was not related to the hand used to make the response. The present data appears to support the hypothesis of the distractor double function in this paradigm: the distractor can act as a competitor for PA in TO trials and as a cue for the target appearance in TFD trials.

6.3. Experiment 5

6.3.1. *Presentation of the Experiment*

In this experiment, we tested the influence of the task on the development of a preparatory strategy by each hemisphere. In Experiments 4, we found the same pattern of responses in the LVF and the RVF resembling the typical RH strategy found in Experiments 1 and 2. This result suggests that the explicit information on distractor probability before each block of trials might have a role in the strategy developed by the LH when a detection task was used. In Experiment 5, we used a location task, in which subjects had to select a response from different alternatives, to explore the role of a more complex task in the LH pattern of results.

6.3.2. *Methods*

Participants. Forty students (12 men and 28 women) of the Institut de Psychologie at Paris Descartes University (Mage = 20.8 years; SD = 2.2; age range: 18-28 years), different from Experiments 1-4, participated in Experiment 5. They had normal or corrected-to-normal vision and no psychiatric or neurological history, learning disability or attentional deficit, assessed by self-report. They were all right-handed (M = 82), evaluated with the Edinburgh Handedness Inventory (Oldfield, 1971). All participants provided informed consent and received course credits for participating in the experiment.

Stimuli. Stimuli were the same as in Experiment 1-4.

Procedure. Experiment 5 was the same to Experiment 1 with the exception of the instruction given to participants. Experiment 5, like in Experiment 4, we use a *D-implicit*

instruction. Precisely, participants were not explicitly informed before each block of trials about the proportion of a distractor appearance.

6.3.3. *Results*

Mean RTs on TO and on TFD trials are shown in Figure 29. See Table 5 for the complete RTs data.

TO trials

Repeated measures ANOVA were calculated on mean RTs, with distractor percentage (0% or d0, 33% or d33, 67% or d67) and visual field (LVF, RVF) as within subjects' factors.

There was an effect of distractor percentage, $F(2, 78) = 75.01$, $p < .001$, $\eta_p^2 = .66$, indicating an increase of RTs when the percentage of distractor trials increased, as in Experiments 1-4. There was a trend towards faster RTs in the RVF (383 ms, *SD* = 81) than in the LVF (393 ms, *SD* = 88), $F(1, 39) = 3.72$, $p = .061$, $\eta_p^2 = .09$. The interaction Distractor percentage x Visual field was not significant, $F(2, 78) = 0.62$, $p = .538$. However, planned comparisons were performed in order to examine the effects of distractor percentage within each visual field since these effects were of theoretical interest. The comparisons revealed that there was no significant difference between the RTs in d67 and the d33, either in the RVF, $F(1, 39) = 1.44$, $p = .238$, or the LVF, $F(1, 39) < 0.01$, $p = .986$. The comparisons also indicated a trend towards faster RTs in the RVF in d0, $F(1, 39) = 3.80$, $p = .059$, $\eta_p^2 = .09$, faster RTs in the RVF in d33, $F(1, 39) = 6.76$, $p = .013$, $\eta_p^2 = .15$, and no significant difference in d67, $F(1, 39) = 0.15$, $p = .697$.

We carried out an ANOVA on the slope values with visual field (LVF, RVF) as within subjects' factor. There was nearly no difference between the slope in the LVF (1.50, *SD* = 1.01) and the RVF (1.50, *SD* = 1.09).

TFD trials

Repeated measures ANOVA were calculated on mean RTs, with distractor percentage (33% or d33, 67% or d67) and visual field (LVF, RVF) as within subjects' factors.

There was a trend towards faster RTs in the RVF (350 ms, *SD* = 75) than in the LVF (358 ms, *SD* = 84), $F(1, 39) = 3.55$, $p = .067$, $\eta_p^2 = .08$. There was no effect of distractor percentage, $F(1, 39) = 0.72$, $p = .401$, and there was a trend toward a significant interaction Visual field x Distractor percentage, $F(1, 39) = 3.18$, $p = .082$, $\eta_p^2 = .08$. Planned comparisons indicated faster RTs in the RVF in d67, $F(1, 39) = 5.84$, $p = .020$, $\eta_p^2 = .13$, and no significant difference in d33, $F(1, 39) = 0.10$, $p = .752$.

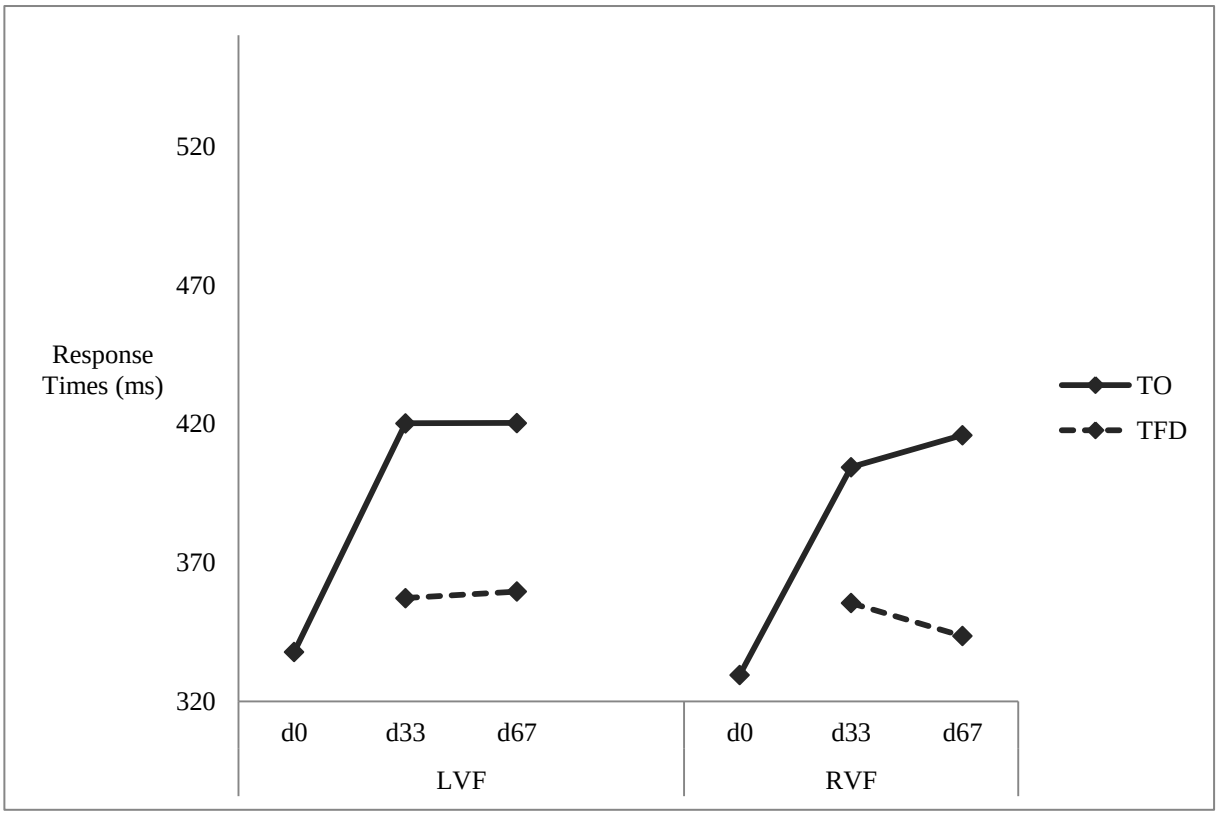

Figure 29: Mean response times in milliseconds (ms) to target-only trials (TO) and to target-following-distractor trials (TFD) in the left visual field (LVF) and in the right visual field (RVF) in Experiment 4.

Error data

We also measured the number of omissions and false alarms. The mean percentage of omissions was 1.37 %, and the mean percentage of false alarms was 0.33%. As the frequency of errors was negligible, no further analysis was carried out with these data.

6.3.4. *Discussion*

In Experiment 5, there was trend towards faster RTs in the RVF than in the LVF for TO trials. In the block with 33% of distractors, RTs were significantly faster in the RVF than in the LVF, as in Experiment 1. This finding might be related to the LH involvement in a task with several response alternatives (Rushworth et al., 1997; Schluter et al., 2001, 1998). However, and most importantly, the pattern of responses for TO trials was similar to the one obtained in Experiment 4. There was a RTs difference between d0 and d33 but no significant difference between the two blocks containing distractors in either visual field. Even though RTs in d67 were slightly slower than in d33 for RVF targets, this difference was not significant. Thus, these findings suggest that the activation of the LH by the location task *per se* cannot account for the *frequency matching* strategy found in previous experiments.

6.4. General discussion

The purpose of this third study was to test the modulation of PA toward a target location by the brain hemispheres when the increasing probability of distractors was learned only from the sequence of trials. The results obtained in Experiments 4 and 5 suggest that the pattern of responses is different when the proportion of distractors is implicitly learned (*D-implicit* instruction) and when this information is explicit (*D-explicit* instruction). Interestingly, the pattern changes only for RVF targets. For targets in the LVF the pattern of RTs is similar to the one obtained with explicit information (Experiments 1 and 2). Precisely, RTs to targets in the LVF were affected by the presence or absence of distractors (difference between d0 and d33), but not by their frequency (lack of difference in RTs between d33 and d67). Without the explicit information about the proportion of distractors, the RH may still be able to maximize the enhancement of PA towards the target at long delays within a trial due to its high temporal predictability at those delays. Still, we may speculate that the temporal probability of the target was learned throughout the sequence of trials owing to the fact that the target temporal probability was not explicit in the instruction.

In contrast, RTs to targets in the RVF differ between *D-implicit* and *D-explicit* instruction. Under a *D-implicit* instruction, RTs in the RVF increased between the blocks with or without distractors (d0 and d33), but they were not affected by their frequency, contrary to

RTs under a *D-explicit* instruction. This finding suggests that the *frequency-matching* pattern of responses obtained for RVF targets in previous experiments may better reflect controlled processes taking place in the LH, rather than automatic processes linked with the computation of events frequencies. In previous experiments, the advance knowledge about the proportion of distractors may activate the LH to develop a suitable preparatory strategy to cope with the increasing probability of distracting events. The *D-explicit* instruction may have been crucial in the LH development of a *frequency matching* strategy to control the allocation of PA toward the target and distractor locations. It can be speculated that this strategy should also be developed in a longer task, with more experimental trials. It might be possible that subjects did not have enough time to notice the increased frequency of distractors in the LAPT, making more difficult for the LH to develop a strategy according to these frequencies. The advanced information about the probability of events may simply accelerate the strategic use of these probabilities to control PA.

The RH modulation of PA in the whole visual field

In the present study, the pattern of responses in the LVF was similar to the RVF. A possible explanation is that the LH was less active to develop a *frequency matching* strategy in the RVF. The lack of information about the proportion of events may presumably delay the development of a strategy in the LH to control PA. Decreasing the control of the LH in PA may reinforce the RH control over the whole visual field, with the consequence of a *maximizing* strategy allocated to the LVF and the RVF. In the present study, the temporal and spatial characteristics of the target were well determined and separated from those of the distractor. The ease to distinguish targets from distractors in the spatial and temporal dimensions may increase the certainty about stimuli appearance. This certainty presumably influenced the predictability of the target event within a trial, and facilitated the development of a *maximizing* strategy in the RH. Our findings suggest that the RH may modulate PA directed to the target location in easy situations, whatever the visual field of its appearance. In agreement with this proposal, several studies have shown that the RH is able to control attention in both sides of space (Corbetta et al., 1993; Perry & Zeki, 2000). The preparatory strategy developed in control areas of the RH can apply in both visual fields.

The strategy presumably developed by the RH was clearly allocated to the entire visual field in a simple detection task (Experiment 4). The pattern of results in the RVF was slightly different to the results in the LVF in a more complex task (Experiment 5). In this

case, there was an advantage of RTs to targets processed by the LH in some blocks, in agreement with the LH involvement in tasks with several response alternatives. Nevertheless, the LH activation by the location task seemed not to be sufficient for activating a different preparatory strategy. This result strengthens the idea that the hemispheric strategies developed to modulate PA are related with the perceptual processing level of information rather than to the motor programming level.

6.5. Conclusion

The findings of this third study suggest that the modulation of PA to a spatial location by the hemispheres partially differs when the distractor probability has to be learned from the sequence of trials than when this probability is informed by an instruction. The *frequency matching* in the RVF was particularly affected when the expected proportion of distractors was not explicit. The LH *frequency matching* might be related with the strategic distribution of PA according to the expected probability of distractors, rather than to the automatic computation of events frequency. The LH difficulty to develop a preparatory strategy and the spatial and temporal predictability or certainty of stimuli appearance may reinforce the relative control of the RH in PA. The reinforcement of the RH activation may result in a *maximizing* strategy applied to the whole visual field.

CHAPTER 7 - Effect of reinforcing instructions on the modulation of PA

7.1. Presentation of the study

The amount of PA directed to a target location is not an all-or-none phenomenon. The attentional activity directed to a spatial location prior to a target occurrence in that location can vary from low to high. The intensity of PA directed to a spatial location can be voluntarily reinforced when appropriately motivated. The reinforcement of the attentional activity directed to a spatial location prior to a target onset can increase the speed and effectiveness of the target processing and decrease the effect of possible distractors (LaBerge et al., 2000). The goal of this fourth study was to examine the capacity of each hemisphere in reinforcing PA towards a target location by means of a simple instruction.

LaBerge et al. (2000) showed that the amount of PA directed to the target could be increased by instructing participants to attend "only" to the target location, creating a condition in which just this location was "of interest" for the subject. They called this instruction "strong", as it encouraged subjects to concentrate high intensities of PA to the target location. The "strong" condition was compared to a "weak" condition (used in previous experiments of this thesis), in which participants were told to respond when the target appeared and to not respond when the distractor appeared. For the "weak" instruction, the target and distractors locations were "of interest" and PA was presumably allocated to both, target and distractor, according to their relative frequency in recent trials. Therefore, in the "weak" instruction the intensity of PA directed to the target was assumed to be lower than in the "strong" instruction condition. According to the theoretical assumptions of the triangular circuit, the "strong" instruction adds additional attentional activity to the target location in the selective control, and only (or mainly) the target site is activated in the modulatory control, preventing the allocation of PA toward distractors. Decreasing PA toward distractors decreases their effect on RTs. Indeed, the results of LaBerge et al. (2000) showed that RTs to the target increased as the probability of distractors increased with the "weak" instruction, whereas there was no effect of distractor probability with the "strong" instruction (see Fig. 13A, pp.46). This result suggests that the reinforcement of PA toward the target with the

instruction increased the signal-to-noise ratio and decreased the effect of distractor probability.

The LH might be particularly involved in reinforcing attentional activity toward a target when distractors are also expected. The LH has been associated to the strategic enhancement of attentional control following an instruction indicating to select the relevant target information from irrelevant distractors (Luks et al., 2007; MacDonald et al., 2000). In attentional demanding tasks, the LH may reinforce the relevant target information in preparation to its occurrence. In addition to this enhancement process, the LH may also reduce the activity arising from expected distractors to decrease their interference on subjects' performance. Consistent with this proposal, the act of enhancing relevant target information from working memory while simultaneously suppressing irrelevant distractors activated frontal areas of the LH (Zhang et al., 2004). Thus, according to these studies, the LH might be crucial in the reinforcement of PA toward a relevant target location and in the reduction of activity arising from distractors when more attentional control is needed.

In this fourth study, we tested the capacity of each hemisphere to reinforce PA with an instruction by comparing RTs in each visual field in two conditions that vary the intensity of attentional activity directed to a target. We manipulated the intensity of PA from low to high by using "weak" and "strong" instructions, respectively. Actually, the "weak" instruction used by LaBerge et al. (2000) corresponds to the *D-implicit* instruction of the experiments presented in Chapter 6. In the present Chapter, we will refer to the *D-implicit* instruction used in Experiments 4 and 5 as *D-implicit-weak* instruction to differentiate it from a *D-implicit-strong* instruction, keeping the same "weak" *vs* "strong" terminology as in the study of reference (LaBerge et al., 2000). The difference in RTs between *D-implicit-weak* and *D-implicit-strong* instructions in each visual field was considered as a direct measure of the capacity of each hemisphere in reinforcing PA toward the target location by means of an instruction. The delay of the target appearance within a trial was highly predictable. We used a location task in which the response to the target was produced by the same hemisphere receiving the perceptual input.

The reinforcement of PA to a target location when distractors are expected might presumably require two processes: the enhancement of activity in target sites and the reduction of activity in distractor sites. In order to examine the role of each hemisphere in these two processes, we compared subjects' performance in two LAPT versions that vary the distractor location. In one version the distractor was central (like in Experiments 1-5) and in

the other version the distractor was lateralized. It was reasoned that both hemispheres might share the reduction of activity in distractor sites when the distractor is central, as it simultaneously projects to both hemispheres. In contrast, each hemisphere should first reduce activity in contralateral distractor sites when the distractor is lateralized, as it primarily projects to only one hemisphere.

If the LH is particularly involved in the instructional reinforcement of attentional activity directed to a target and in reducing the activity directed to distractors, we should obtain faster RTs and less effect of distractors in the RVF, for the *D-implicit-strong* condition when compared to the *D-implicit-weak* condition, regardless the distractor type (central or lateral).

Experiment 6

7.2. Methods

Participants. Sixty-six students (22 men and 44 women) of the Institut de Psychologie at Paris Descartes University (M_{age} = 21.3 years; *SD* = 3.4; age range: 18-38 years), different from Experiments 1-5, participated in Experiment 6. They had normal or corrected-to-normal vision and no psychiatric or neurological history, learning disability or attentional deficit, assessed by self-report. They were all right-handed (*M* = 85), evaluated with the Edinburgh Handedness Inventory (Oldfield, 1971). All participants provided informed consent and received course credits for participating in the experiment.

Stimuli. For the version of the LAPT with a central distractor, stimuli are the same as in Experiments 1-5. For the version of the LAPT with a lateral distractor, there was a modification of the stimulus display. This modification rotates the stimulus display 90° clockwise in each visual field to present lateralized targets and distractors (see Fig. 30). Thus, the stimulus display consisted of a fixation plus sign (+), subtending about 0.4° x 0.4°, in the center of the screen, and three empty lateral boxes that were arranged vertically, on the left and on the right of fixation. Each lateral display was centered 2° (20 mm) from fixation and subtended 4.8° of visual angle (4.8 cm). In each visual field, the empty boxes were separated from each other by a space of 1.2° of visual angle (12 mm). The target consisted of a black

square of 0.7° of visual angle (7 mm), and could appear in the central box of the three empty vertically arranged boxes, in the left or in the right visual fields. The distance between the center of the screen and the center of the target subtended 2° of visual angle. This means that the eccentricity of the target (distance between the center of the display and the closest extremity of the target) was 1.65°, as in the previous version of the LAPT. The distractor was represented by the same black square appearing in one of the boxes located above or below the central box, in the left or in the right. Note that the empty boxes containing the target and the distractor were separated by the same distance in the versions with central and lateral distractors (12 mm). More importantly, the target had the same eccentricity in the LAPT version with central and with lateral distractors.

Procedure. The stimuli presented in the LAPT version with central distractor are shown in Figure 21 (pp. 84) and those in the LAPT version with lateral distractor are shown in Figure 30. Only one LAPT version was used per participant (central or lateral distractor), leaving thirty-three subjects for each version. The procedure of Experiment 6 was equivalent to Experiment 1 with the following exceptions. In targets-following-distractor trials in the lateral distractor condition, the target appeared in the same visual field as the distractor 50% of the time, and in the opposite visual field the other 50%. Also, participants were not informed about the proportion of distractors before each block of trials. Instead, there were two possible conditions, defined by different instructions. The instructions were carefully written.

In both conditions (*D-implicit-weak* and *D-implicit-strong*) subjects were explicitly instructed to fixate the center of the screen during the whole trial, and to respond to the target as quickly and accurately as possible. Participants were instructed to press the key “s” of the keyboard with the index finger of the left hand when the target appeared on the left (central distractor) or within the central box of the three empty boxes on the left (lateral distractor), and the key “m” with the index finger of the right hand when the target appeared on the right (central distractor) or within the central box of the three empty boxes on the right (lateral distractor). The *D-implicit-weak* instruction slightly changed for the central and lateral distractor LAPT versions. Participants were instructed to not respond when the black square appeared in the central box (central distractor), or when it appeared above or below the central box on the left or on the right (lateral distractor), without any further information about the proportion of distractors.

The *D-implicit-strong* instruction also slightly changed for the central and lateral distractor LAPT versions. In the *D-implicit-strong* condition of the LAPT version with central distractors, participants were instructed to focus their attention in the right and left empty boxes and to press the appropriate key when the black square appeared in one of them. In the *D-implicit-strong* condition of the LAPT version with lateral distractors, participants were instructed to focus their attention in the centered right and left empty boxes and to press the appropriate key when the black square appears in one of them. The *D-implicit-strong* instructions were repeated before the beginning of each block of trials, in order to reinforce the amount of attention directed to the target location. Each subject ran the *D-implicit-strong* condition in a period between 7 and 15 days after they ran the *D-implicit-weak* condition.

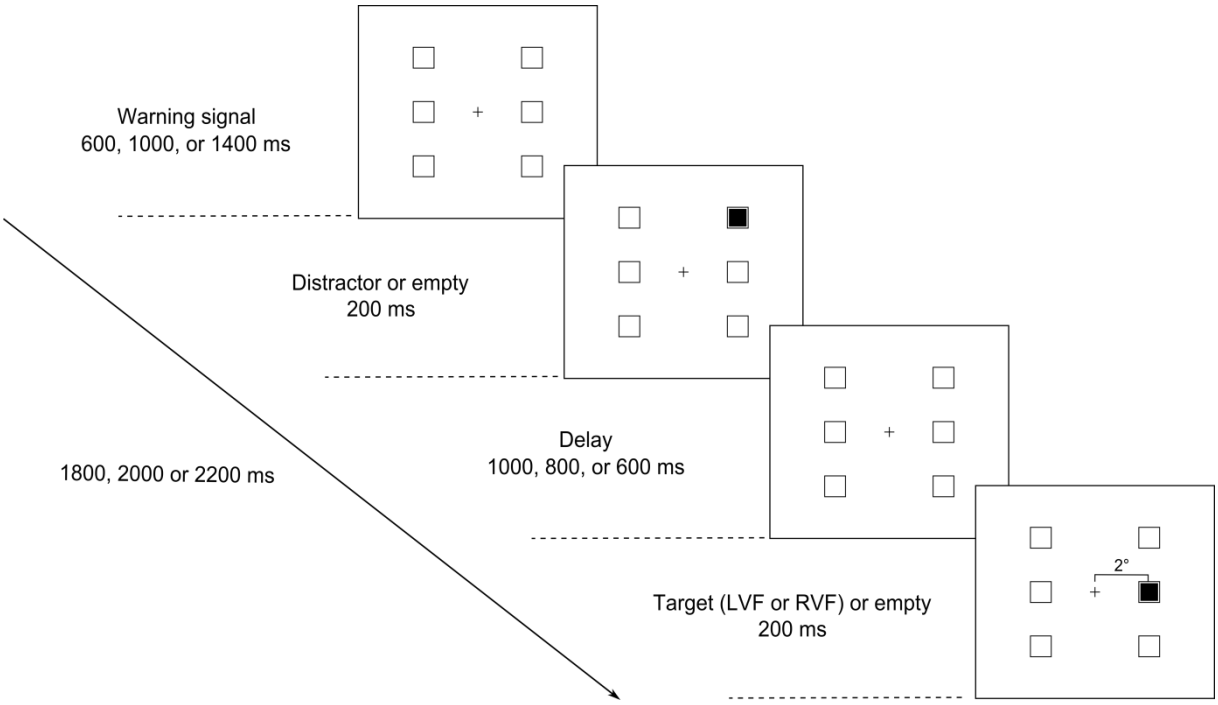

Figure 30: Example of the sequence of stimuli presented in a trial in the peripheral distractor condition of Experiment 6. The target display showed a black square in the central box equally often in the right visual field (RVF) or in the left visual field (LVF). The distractor display showed a black square equally often in the boxes located above or below the target, in the LVF or in the RVF. In targets-following- distractor trials, the target appeared in the same visual field as the distractor 50% of the time, and in the opposite visual field the other 50%. In the central distractor condition (Fig. 21, pp. 84) the target display also showed a black square equally often in the right visual field (RVF) or in the left visual field (LVF). The distractor display showed a black square in the

box located in the center of the screen. In targets-following- distractor trials, the target appeared after the central distractor in the LVF 50% of the time, and in the RVF the other 50%.

7.3. Results

TO trials

Repeated measures ANOVA were calculated on mean RTs, with distractor type (central, lateral) as between subjects' factor, and distractor percentage (0% or d0, 33% or d33, 67% or d67), visual field (LVF, RVF), and instruction (D-implicit-weak, D-implicit-strong) as within subjects' factors. Mean RTs on TO trials are shown in Figure 31. See Table 6 for the complete RTs data.

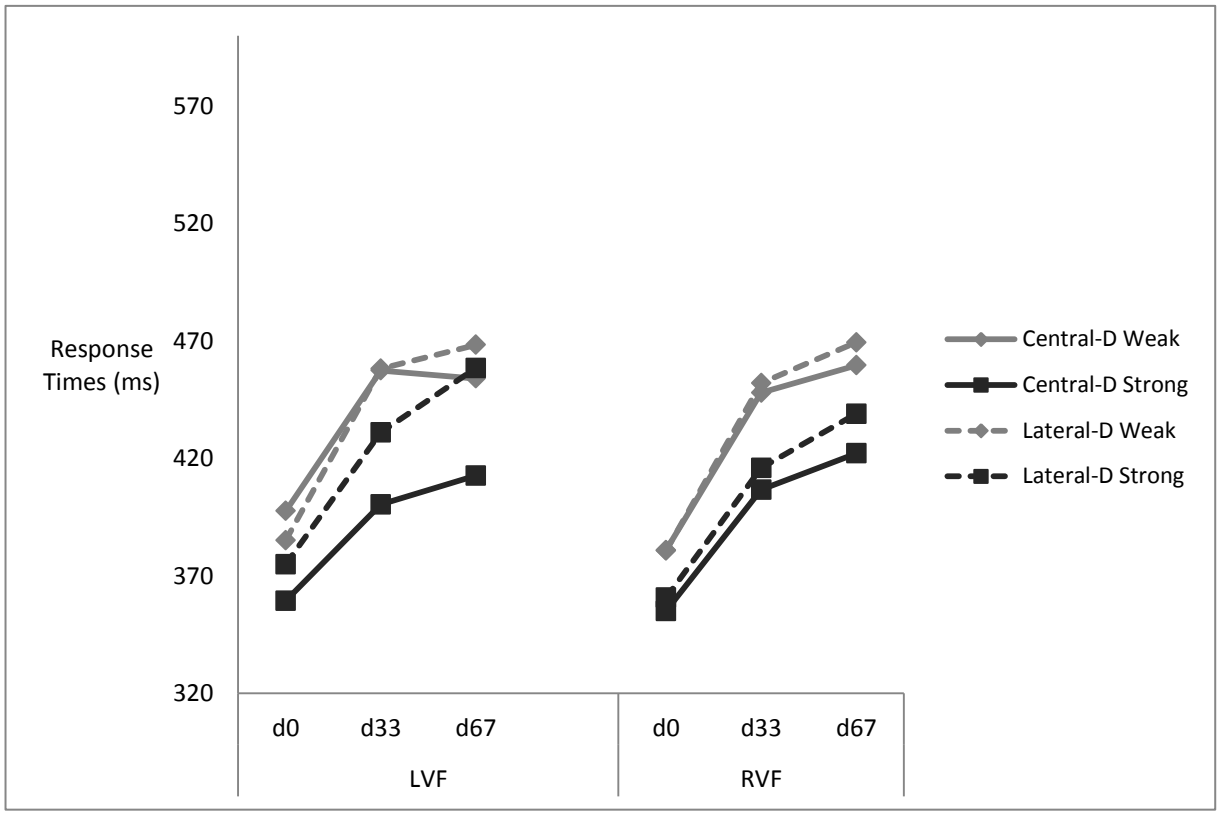

Figure 31: Mean response times in milliseconds (ms) to target-only trials as a function of distractor probability (d0, d33, and d67) for each distractor type (Central-D; Lateral-D) under the instruction conditions D-unknown-weak (Weak) and D-unknown-strong (Strong) in the left visual field (LVF) and in the right visual field (RVF) in Experiment 6.

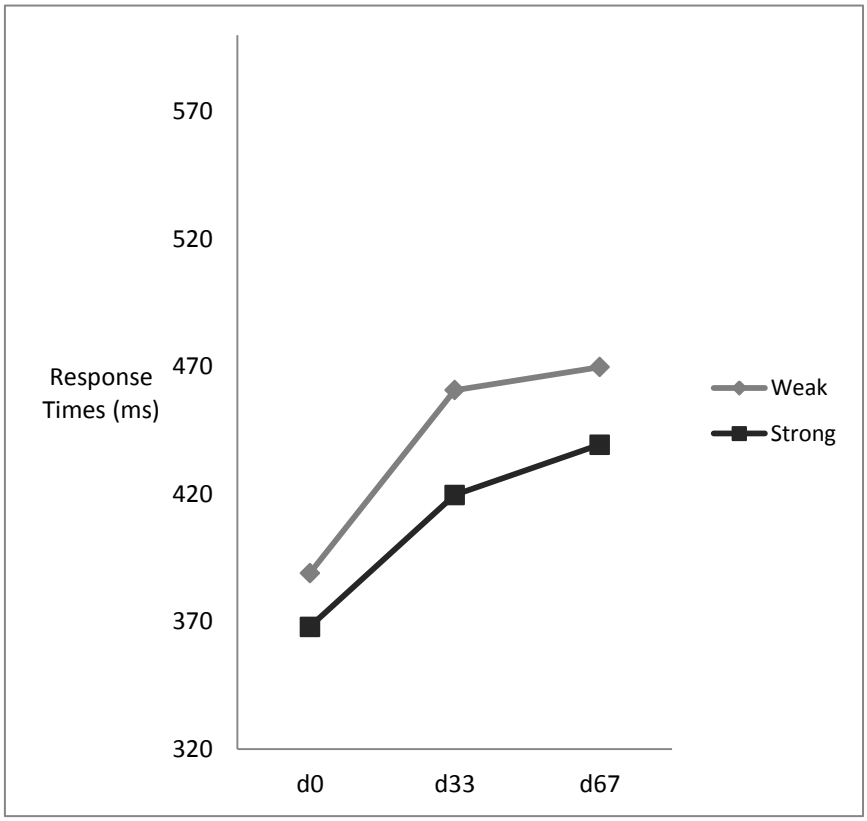

Figure 32: Mean response times in milliseconds (ms) to target-only trials for the D-unknown-weak (Weak) and D-unknown-strong (Strong) instruction conditions in each bloc of trials (d0, d33 and d67) of Experiment 6.

There was an effect of instruction, $F(1, 64) = 23.35$, $p < .001$, $\eta_p^2 = .28$, indicating faster RTs in the strong instruction condition (409 ms, *SD* = 88) than in the weak instruction condition (440 ms, *SD* = 84). There was an effect of distractor percentage, $F(2, 128) = 192.04$, $p < .001$, $\eta_p^2 = .75$, indicating an increase of RTs when the percentage of distractor trials increased. The interaction Instruction x Distractor percentage (Fig. 32) was significant, $F(2, 128) = 4.39$, $p = .014$, $\eta_p^2 = .06$ (see slopes analyses). The interaction Instruction x Distractor percentage x Visual Field was not significant, $F(2, 128) = 0.91$, $p = .407$ (Fig. 33).

There was also a significant interaction between Instruction x Visual field x Distractor type, $F(1, 64) = 4.00$, $p = .050$, $\eta_p^2 = .06$ (see Fig. 34). Planned comparisons revealed that, under D-implicit-strong instruction, RTs were significantly faster in the RVF (405 ms, *SD* = 85) that in the LVF (421 ms, *SD* = 89) with a peripheral distractor, $F(1, 64) = 9.29$, $p = .003$, $\eta_p^2 = .13$, but were not significantly different between RVF (407 ms, *SD* = 87) and LVF (403 ms, *SD* = 91) with the central distractor, $F(1, 64) = 0.54$, $p = .466$. Under D-implicit-weak

instruction there was no significant difference in RTs between the RVF and the LVF, with the peripheral, $F(1, 64) = 0.24$, $p = .629$, as the central distractor, $F(1, 64) = 0.21$, $p = .645$.

We carried out an ANOVA on the slope values with distractor type (central, peripheral) as between subjects' factor, and visual field (LVF, RVF) and instruction (D-implicit-weak, D-implicit-strong) as within subjects' factors. The only significant main effect was instruction, $F(1, 64) = 4.55$, $p = .037$, $\eta_p^2 = .07$, indicating a smaller slope of RTs in the D-implicit-strong instruction (1.18, *SD* = 0.84) than in the D-implicit-weak instruction (1.41, *SD* = 0.92) .

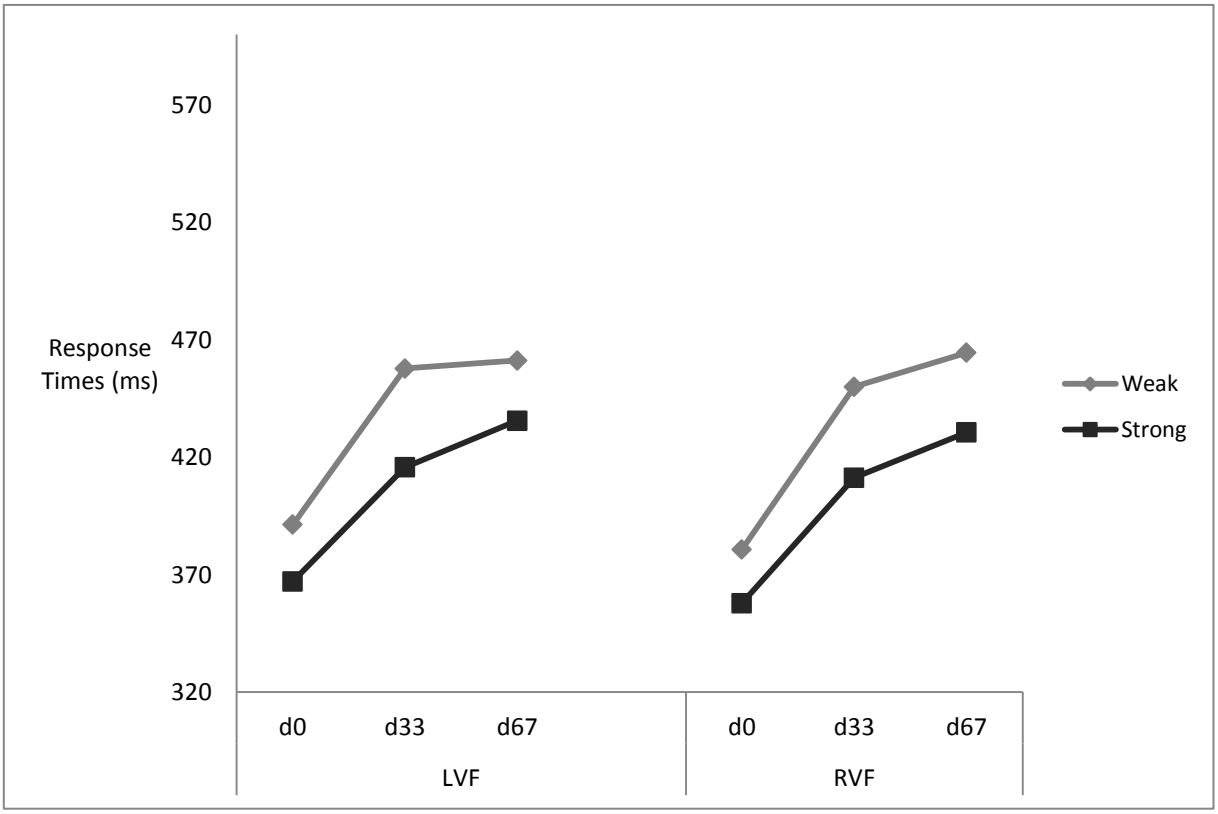

Figure 33: Mean response times in milliseconds (ms) to target-only trials as a function of distractor probability (d0, d33, and d67) in the left visual field (LVF) and in the right visual field (RVF) under D-unknown-weak (Weak) and D-unknown-strong (Strong) instruction conditions in Experiment 6.

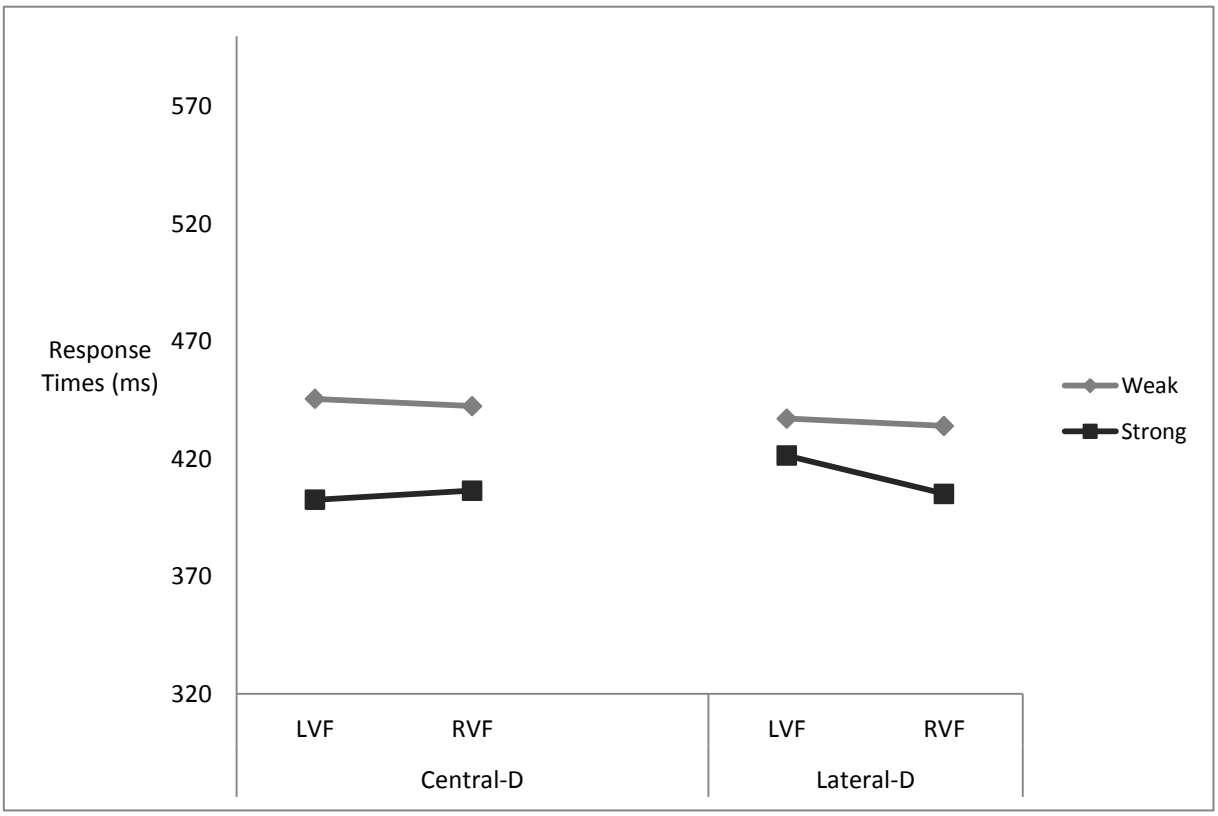

Figure 34: Mean response times in milliseconds (ms) to target-only trials for each distractor type (Central-D; Lateral-D) under D-unknown-weak (Weak) and D-unknown-strong (Strong) instruction conditions in the left visual field (LVF) and in the right visual field (RVF) in Experiment 6.

TFD trials

Repeated measures ANOVA were calculated on mean RTs, with distractor type (central, peripheral) as between subjects' factor, and distractor percentage (33% or d33, 67% or d67), visual field (LVF, RVF), and instruction (D-implicit-weak, D-implicit-strong) as within subjects' factors. Mean RTs on TFD trials are shown in Figure 35. See Table 6 for the complete RTs data.

There was an effect of instruction, $F(1, 64) = 45.59$, $p < .001$, $\eta_p^2 = .42$, indicating faster RTs in the strong (379 ms, *SD* = 85) than in the weak instruction condition (424 ms, *SD* = 80). There was an effect of distractor percentage, $F(1, 64) = 23.11$, $p < .001$, $\eta_p^2 = .27$, with faster RTs in d67 (394 ms, *SD* = 83) than in d33 (409 ms, *SD* = 88). There was a significant effect of visual field, $F(1, 64) = 5.71$, $p = .020$, $\eta_p^2 = .08$, revealing faster RTs for RVF (397 ms, *SD* = 83) than LVF targets (406 ms, *SD* = 88). The interaction Instruction x Distractor percentage was significant, $F(1, 64) = 13.52$, $p < .001$, $\eta_p^2 = .17$. Planned comparisons

revealed that RTs were significantly faster in d67 (411 ms, *SD* = 79) than in the d33 (437 ms, *SD* = 80) under the weak instruction, $F(1, 64) = 38.08$, $p < .001$, $\eta_p^2 = .38$, although the difference between d67 (376 ms, *SD* = 83) and d33 (382 ms, *SD* = 88) was not significant under the strong instruction, $F(1, 64) = 1.46$, $p = .232$.

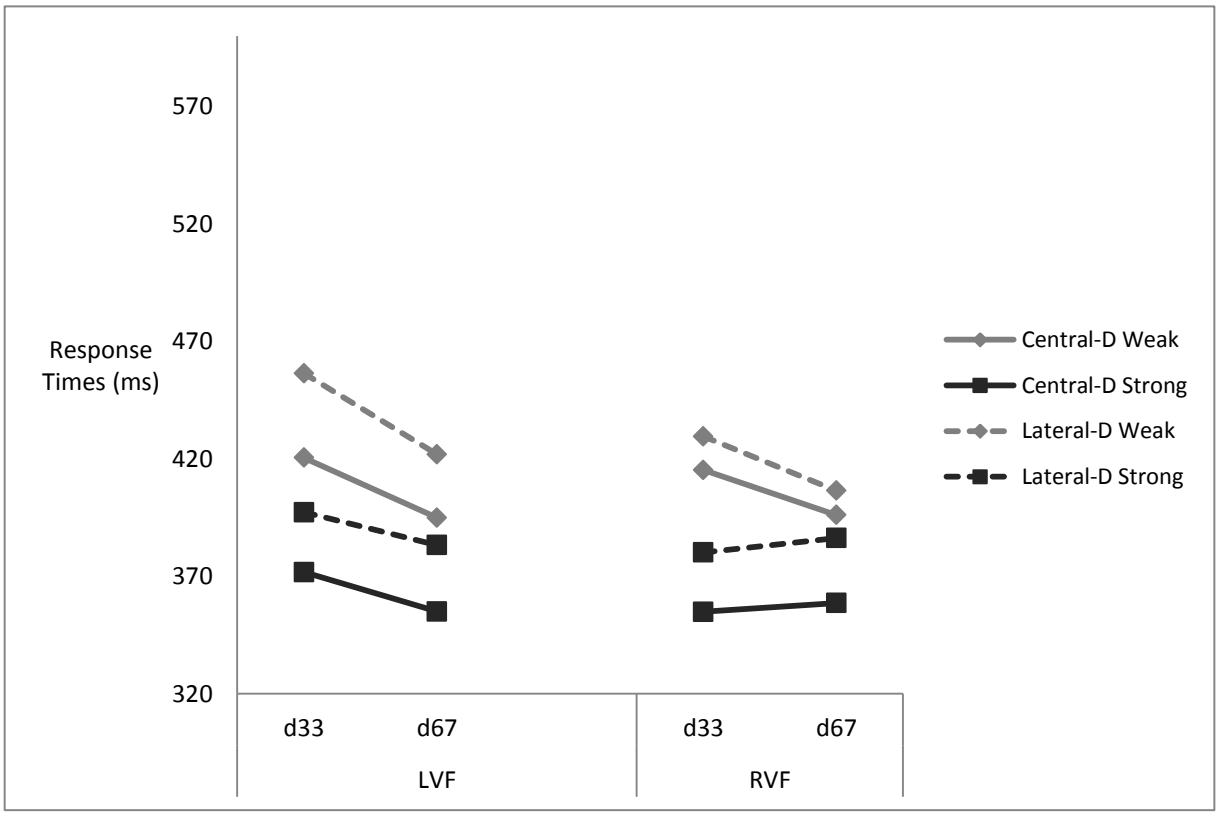

Figure 35: Mean response times in milliseconds (ms) to target-following-distractor trials for each distractor type (Central-D; Lateral-D) under the instruction conditions D-unknown-weak (Weak) and D-unknown-strong (Strong) in the left visual field (LVF) and in the right visual field (RVF) in Experiment 6.

There was an interaction between visual field and distractor percentage, $F(1, 64) = 7.50$, $p = .008$, $\eta_p^2 = .10$. Planned comparisons revealed faster RTs in d67 (395 ms, *SD* = 83) than in d33 (418 ms, *SD* = 93) in the LVF, $F(1, 64) = 40.04$, $p < .001$, $\eta_p^2 = .38$,but the difference between d67 (393 ms, *SD* = 83) than in d33 (401 ms, *SD* = 83) was not significant in the RVF, $F(1, 64) = 2.99$, $p = .089$. The comparisons also revealed that RTs in the RVF were faster than in the LVF in the block with 33% of distractors, $F(1, 64) = 8.73$, $p = .004$, $\eta_p^2 = .12$, although there was no significant difference between the RVF and the LVF in the block with 67% of distractors, $F(1, 64) = 0.28$, $p = .60$.

Error data

We also measured the number of omissions and false alarms corresponding to each condition. For the D-implicit-weak instruction condition the mean percentage of omissions was 0.10%, and the mean percentage of false alarms was 0.07%. For the D-implicit-strong instruction condition the mean percentage of omissions was 0.20%, and the mean percentage of false alarms was 0.04%. As the frequency of errors was negligible for both conditions, no further analysis was carried out with these data.

Table 6

Mean response times in milliseconds and standard deviations (in parentheses) in Experiment 6 for TO trials and TFD trials, as a function of the distractor type (central, lateral) instruction (D-implicit-weak, D-implicit-strong) and the visual field of the target (LVF, RVF) in each block of trials (d0, d33, d67).

Distractor Type	Instruction	VF	TO			TFD	
			d0	d33	d67	d33	d67
Central	D-unknown-weak	LVF	396 (82)	457 (95)	454 (96)	421 (95)	395 (86)
		RVF	381 (73)	448 (89)	460 (95)	415 (72)	396 (79)
	D-unknown-strong	LVF	359 (81)	400 (87)	413 (97)	372 (102)	355 (80)
		RVF	355 (76)	407 (83)	422 (87)	355 (77)	359 (86)
Lateral	D-unknown-weak	LVF	385 (54)	458 (60)	468 (72)	456 (70)	422 (78)
		RVF	381 (57)	452 (63)	469 (61)	430 (72)	406 (73)
	D-unknown-strong	LVF	375 (67)	431 (82)	458 (95)	397 (84)	383 (78)
		RVF	361 (54)	416 (90)	439 (87)	380 (86)	386 (91)

7.4. Discussion

This fourth study aimed to examine the capacity of each hemisphere in the reinforcement of PA directed to the target location by means of a simple instruction. We compared the performance of subjects under two conditions differentiated by the instruction, one in which participants had to respond to the target and not to the distractor (weak instruction), and one in which they had to focus and respond to the target (strong instruction).

The intensity of PA directed to the target was assumed to be low in the *D-implicit-weak* instruction condition, whereas the intensity of PA was assumed to be higher in the *D-implicit-strong* instruction, due to an attentional reinforcement toward the target location.

The results for targets appearing alone within a trial (TO) showed that RTs were faster with the *D-implicit-strong* instruction than with the *D-implicit-weak* instruction. The advantage in RTs for the *D-implicit-strong* instruction suggests that participants were able to increase the intensity of PA toward the target when motivated by an appropriate instruction. There was an interaction between instruction and distractor percentage. The analysis of the slope of RTs indicated that distractors had a lower interference in the *D-implicit-strong* than the *D-implicit-weak* instruction condition. This result is consistent with the assumptions of the triangular circuit theory stating that the strong instruction adds additional attentional activity to the target location in the selective control module. As a consequence, the target is processed faster under the *D-implicit-strong* instruction. However, the effect of distractors' probability did not decrease with the *D-implicit-strong* instruction in the LAPT as much as in the APT. More precisely, we did not obtain a near zero slope of RTs with the LAPT, like in the APT (LaBerge et al., 2000; Experiment 2), suggesting that the strong instruction in the LAPT was not as efficient as in the APT. It is worthy to mention that there are several differences with the paradigm of reference. In the APT strong instruction condition, participants were instructed to focus their attention on one location only (the center square, where the target could appear), whereas, in the LAPT strong instruction condition, participants were told to focus their attention on two locations (the center squares of the display in the LVF and in the RVF). The reinforcement of PA toward two lateral locations may presumably be more difficult than the reinforcement of PA toward one central location. The modulatory control of PA may not efficiently activate the target location in the LAPT, owing to the difficulty of the task. As a consequence, the distractors still compete for PA in the modulatory control. Thus, the *D-implicit-strong* instruction in the LAPT might enhance the amount of PA toward the lateralized target but it might not completely cancel the effect of distractors percentage, presumably because of the difficulty to focus attention in two different locations.

There was a RVF advantage with the *D-implicit-strong* instruction, but only when the distractor was lateralized. When the distractor was located at fixation, there was no visual field advantage. These results may not be in total agreement with our hypothesis stating that the LH is especially involved in the instructional reinforcement of attentional activity directed

to a target and in reducing the activity directed to distractors, whatever the distractor location. A more plausible interpretation of our findings is that both hemispheres were capable of enhancing PA to a target spatial location with the instruction but the LH was particularly recruited for reducing the interference arising from distractors in a more attentional demanding situation (*D-implicit-strong*). It has been demonstrated that it is more efficient for the hemispheres to operate collaboratively when the task is more demanding (Hellige, 1993). This means that there might be a benefit in distributing information processing across hemispheres in demanding situations. The cooperation is faster when the stimuli to be processed are simultaneously projected to both hemispheres. In the intact brain, both hemispheres may coordinate their activities when simultaneously presented with the same stimuli to get the control for those components of processing that each hemisphere handles best. In our study, both hemispheres had simultaneous access to the distractor when the distractor was centrally located. The cooperation of both hemispheres in the central distractor condition may allow the LH to reduce the effect of possible distractors, while the RH can still control the enhancement of attention toward the LVF target. In contrast, when the distractor is projected to one hemisphere at a time (lateral distractor), the cost in RTs for LVF targets might be associated with the need to transfer information across hemispheres to coordinate the activities in a more demanding situation.

The RVF advantage in the condition with lateral distractor may also be related with the possible role of the LH in PA under uncertainty. A particular difference between the LAPT version with central and with lateral distractor is the number of possible locations in which an event could occur. Whereas there were three possible locations in the central distractor version, there were six possible locations in the lateral version. The increase of locations in which an event could appear should increase the spatial uncertainty in a given task. The stimuli spatial uncertainty in the version with six locations to scan may contribute to the LH recruitment. Thus, the spatial uncertainty about stimuli appearance in the LAPT version with lateral distractors may reinforce the LH activation.

For targets that appeared after a distractor (TFD), there was a main effect of instruction, indicating faster RTs with the *D-implicit-strong* instruction than with the *D-implicit-weak* instruction. There was less effect of distractor percentage with the *D-implicit-strong* instruction than with the *D-implicit-weak* instruction, suggesting that the concentration of higher intensities of attention at the target location decreased the effect distractors percentage. Still, RTs in TFD trials were faster than in TO trials, suggesting that subjects were

able to use the distractor as a warning cue indicating the appearance of the target. Interestingly, there was less effect of distractor percentage in the RVF than in the LVF, regardless the distractor location (central or lateral). A possibility is that the reduction of activity toward the distractor by the LH contributed to decrease the effect of distractor percentage in the RVF.

Focusing attention in a small area of the visual field and the LH

In daily life, individuals control the size of the spatial attending area according to the goal to be achieved and task demands. This means that the area of the visual field in which attentional activity can be directed is not static. Individuals can spread PA over a large area or focus high amounts of PA over a small area in the visual field (Eriksen & Yeh, 1985). Narrowing attention to a particular target location was shown to cancel other influences on attention, like for example the influence of nearby distractors in the target display, when targets and distractors are presented together (Eriksen & St. James, 1986), or the influence of recent trial containing distractor events, when targets and distractors are not presented together, like in the LAPT.

The ability of narrowing attention to a specific spatial location has been traditionally related to the LH. Studies using hierarchical visual stimuli (Navon, 1977) claim that the LH is superior for controlling the allocation of attention on local levels of visuospatial information (see Chapter 3). The LH may be particular involved in focusing attention to a specific small area in the visual field. The results obtained in our study might also be related to this LH capacity because, in the *D-implicit-strong* instruction condition, participants were explicitly asked to focus their attention on the spatial locations in which the target was expected to occur. In this condition, the LH may be recruited to reinforce the amount of attentional resources allocated in a small area of the visual field.

7.5. Conclusion

The findings of this study showed that the distribution of PA in the visual field may be regulated by the motivational properties of an instruction. Both hemispheres might be capable of enhancing the amount of attentional activity directed to a target location by means of an instruction. In addition to this enhancement capacity by both hemispheres, the LH might be

particularly involved in the reduction of activity directed to distractors in more demanding situations (number of locations to scan).

CHAPTER 8: Effect of perceptual difficulty in the modulation of PA

8.1. Presentation of the study

PA increases the speed and effectiveness of a target processing, preventing subjects of being disturbed by distracting events. The influence of a distractor was shown to increase as its proximity from a relevant target location decreases (Eriksen & St. James, 1986). The proximity of the target and distractor locations may influence the preparatory strategy developed to respond to the target. In other words, the modulation of PA directed to a target spatial location may also be determined by the perceptual difficulty. The aim of the present study was to investigate the influence of the perceptual difficulty, specifically the spatial proximity between the distractor and the target, on the modulation of PA by the brain hemispheres.

The results of our previous studies suggest that PA in the RH is modulated by the temporal predictability or certainty of expected events. The RH may base its preparatory strategy on events with high temporal predictability, and the RH preparatory strategy was affected when the delays of targets and distractors overlapped (Experiment 3). As temporal and spatial dimensions might be closely related in the preparatory processes of the RH (Brunia et al., 2000; Coull et al., 2000; Vallesi & Crescentini, 2011; Vallesi et al., 2008), the question is whether the RH is also sensitive to the relative predictability of stimuli in space. In the LAPT versions used until here, the spatial location of the target and the distractor were easily distinguishable from each other. The deployment of the RH strategy may have been facilitated by the spatial and temporal predictability of the stimuli, in spatial and temporal dimensions. Hence, the RH might be particularly involved in modulating PA to a target when its perceptual discrimination from a distractor is relatively easy.

In contrast to the RH, the LH may modulate PA when the discrimination of the target is more difficult to achieve. Increasing the perceptual difficulty in a given task may increase the recruitment of the LH to develop a suitable preparatory strategy (Luks et al., 2007; MacDonald et al., 2000). The results obtained in Experiment 3 suggest that the LH was more

suited than the RH to develop a preparatory strategy when the proximity of the temporal intervals between targets and distractors decreased, increasing the stimuli temporal uncertainty within a trial. The temporal uncertainty of stimuli might have increase the difficulty to select the relevant target information within a trial, reinforcing the involvement of the LH in PA. The LH might be recruited to control the allocation of PA to target information when its selection from irrelevant information is relatively hard (Zhang et al., 2004).

We designed Experiment 7 to examine the role of the perceptual difficulty to discriminate stimuli locations in the modulation of PA by the brain hemispheres. When the target location is well separated from the distractor location the certainty about their positions in space is relatively high, decreasing perceptual difficulty. When target and distractor locations overlap, the spatial certainty decreases, increasing perceptual difficulty. We developed a LAPT version in which the proximity of targets and distractors spatial locations was manipulated. There were two experimental conditions: in the easy condition, target and distractor locations did not overlap; in the hard condition, they partially overlapped. The spatial uncertainty increased when the target and distractor locations partially overlap, producing a stronger perceptual conflict or interference. Targets and distractors never appeared together within a trial and their temporal delay of appearance was highly predictable. The results of our previous studies suggest that the explicit advance information about the proportion of distractors within a block of trials (*D-explicit*) might be sufficient to activate the LH preparatory strategy (Experiments 1and 2). We used a *D-implicit-weak* instruction, so that visual field effect might be related to task perceptual difficulty rather than to the expectation of distractor frequency, given by an instruction.

If the strategy developed by each hemisphere to modulate PA toward a spatial location is also related to the perceptual difficulty to discriminate targets from distractors, we should obtain a different pattern of responses in the LVF and the RVF depending on the experimental condition. In the easy condition, we should obtain a similar pattern of responses than in experiments in which the target has a high temporal and spatial predictability and implicit instructions (Experiments 4 and 5). Precisely, we should obtain an increase of RTs between the blocks with and without distractors, and a lack of difference in RTs between the two blocks containing distractors (*maximizing* strategy) in the whole visual field. The RH should be able to maximize PA towards the target in a condition in which there is a high spatial and temporal certainty about its appearance, that is, when the target is highly predictable in spatial

and temporal dimensions. The LH should not develop the frequency matching strategy in the absence of explicit instruction on the percentage of distractors. In the hard condition, we may find a similar pattern of responses as in Experiment 3, in which the uncertainty about the target appearance was high. Stimuli spatial uncertainty should prevent the RH to develop its *maximizing* strategy. Then, a gradual increase of RTs as a function of distractor probability in the whole visual field, owing to the LH modulation of PA according to the frequency of events (*frequency matching* strategy), should be obtained. If the LH needs to transfer information to the RH to modulate incoming LVF sensory input (see Fig. 27), we should also obtain faster RTs in the RVF compared to the LVF in the hard condition.

Experiment 7

8.2. Methods

Participants. Fifty two students (20 men and 32 women) of the Institut de Psychologie at Paris Descartes University (M_{age} = 20.8 years; *SD* = 3.6; age range: 18-39 years), different from Experiments 1-6, participated in Experiment 7. They had normal or corrected-to-normal vision and no psychiatric or neurological history, learning disability or attentional deficit, assessed by self-report. They were all right-handed (*M* = 86), evaluated with the Edinburgh Handedness Inventory (Oldfield, 1971). All participants provided informed consent and received course credits for participating in the experiment.

Stimuli. The stimulus display consisted of a fixation plus sign (+), which subtended about 0.4° x 0.4° of visual angle, and two empty lateral rectangles centered 2° (20 mm) from fixation, on the left and on the right. Each rectangle was arranged vertically and subtended about 2.4° x 0.8°. The total display was centered on the middle of the screen. The target consisted of a black square of 0.7° of visual angle (7 mm), and appeared in the center of one of the two empty lateral rectangles. The distance between the center of the screen and the center of the target subtended 2° of visual angle. This means that the eccentricity of the target (distance between the center of the display and the closest extremity of the target) was 1.65°, like in the other LAPT versions. The distractor was a black square of the same size of the target, which could appear above or below the center of one of the lateral rectangles. In the Easy condition, the distance between the center of the rectangle and the center of the

distractor was 7 mm. In the Hard condition, the distance between the center of the rectangle and the center of the distractor was 3.5 mm. Note that in the Hard condition the location in which the distractor might appear overlapped partially with the location in which the target might occur.

Procedure. The stimuli presented in a trial are shown in Figure 36.The procedure was similar to Experiment 1 with the following exceptions. Participants were instructed to press the key "s" of the keyboard with the index finger of the left hand when the black square appeared in the center of the empty rectangle on the left, and the key "m" with the index finger of the right hand when the target appeared in the center of the empty rectangle on the right. Participants were also instructed to not respond when the black square appeared above or below the center of the empty rectangle on the left or on the right, without any further information about the proportion of distractors *(D-implicit* instruction). Subjects performed the Easy and Hard condition in the same experimental session and the order of presentation was balanced between subjects.

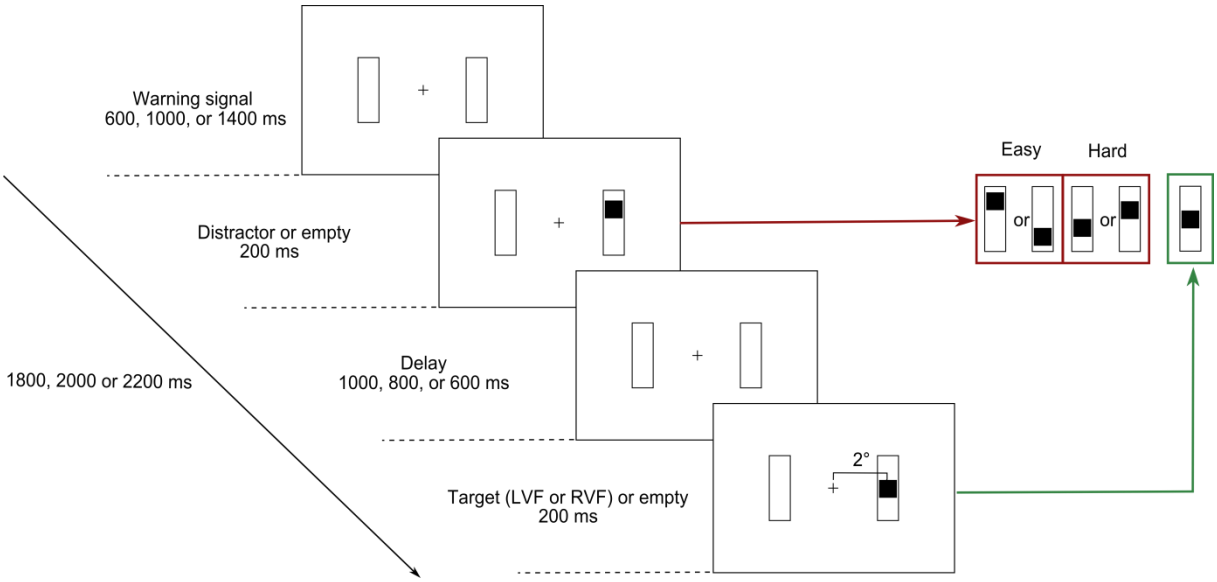

Figure 36: Example of the sequence of stimuli presented in a trial of Experiment 7. The target display showed a black square in the center of the rectangle equally often in the right visual field (RVF) or in the left visual field (LVF). The distractor display showed a black square equally often above or below the target location inside the rectangle, in the LVF or in the RVF. In targets-following- distractor trials, the target appeared in the same visual field as the distractor 50% of the time and in the opposite visual field the other 50%.

8.3. Results

TO trials

Repeated measures ANOVA were calculated on mean RTs, with distractor percentage (0% or d0, 33% or d33, 67% or d67) visual field (LVF, RVF), and difficulty (easy, hard) as within subjects' factors and order of presentation (easy-hard, hard-easy) as between subjects' factor. Mean RTs on TO trials are shown in Figure 37. See Table 7 for the complete RTs data.

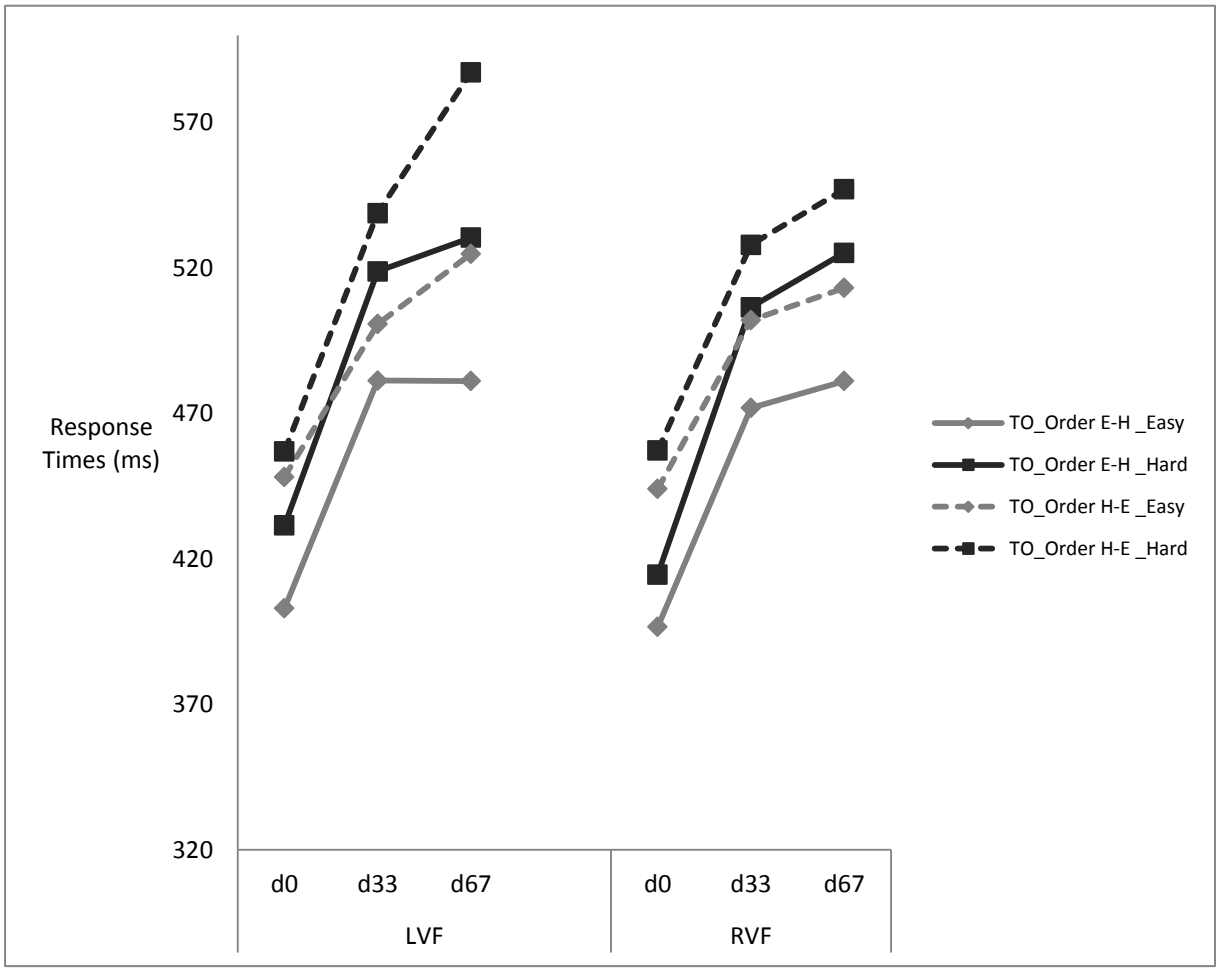

Figure 37: Mean response times in milliseconds (ms) to target-only trials (TO) on the easy and hard conditions for each order of presentation (easy/hard [E-H], hard/easy [H-E]) in the left visual field (LVF) and in the right visual field (RVF) in Experiment 7.

There was an effect of difficulty, $F(1, 50) = 25.97$, $p < .001$, $\eta_p^2 = .34$, indicating faster RTs in the easy (471 ms, *SD* = 88) than in the hard condition (504 ms, *SD* = 106). There was

also an effect of distractor percentage, $F(2, 100) = 152.27$, $p < .001$, $\eta_p^2 = .75$, indicating an increase of RTs when the percentage of distractor trials increased. The interaction Difficulty x Distractor percentage was also significant, $F(2, 100) = 4.68$, $p = .011$, $\eta_p^2 = .09$ (see Fig. 38). Planned comparisons revealed that RTs were significantly slower in d67 than in the d33 in the hard condition, $F(1, 50) = 13.25$, $p = .001$, $\eta_p^2 = .21$, although this difference did not reach significance in the easy condition, $F(1, 50) = 3.73$, $p = .059$.

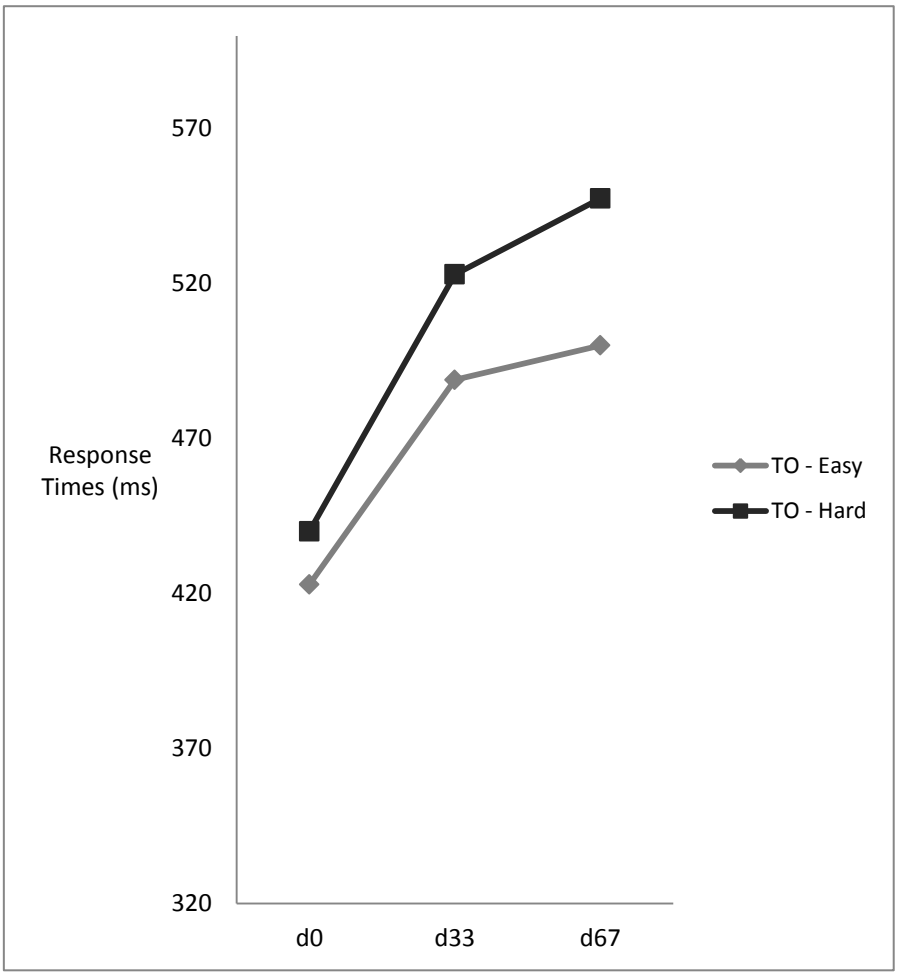

Figure 38: Mean response times in milliseconds (ms) to target-only trials (TO) for the easy and hard conditions in each bloc of trials (d0, d33 and d67) of Experiment 7.

There was a significant main effect of visual field, $F(1, 50) = 5.4$, $p = .024$, $\eta_p^2 = .1$, with faster RTs in the RVF (482 ms, *SD* = 94) than in the LVF (492 ms, *SD* = 103). There was a trend towards a significant interaction Difficulty x Visual field, $F(1, 50) = 3.36$, $p = .073$, $\eta_p^2 = .06$. Planned comparisons indicated faster RTs in the RVF (496 ms, *SD* = 102) than in the LVF (511 ms, *SD* = 111) in the hard condition, $F(1, 50) = 7.34$, $p = .009$, $\eta_p^2 = .13$,

although the difference between RVF (468 ms, *SD* = 84) and LVF (473 ms, *SD* = 92) was not significant in the easy condition, $F(1, 50) = 1.32$, $p = .256$.

The interaction Difficulty x Distractor percentage x Visual field, was not significant $F(2, 100) = 0.50$, $p = .606$. Interestingly, there was a triple interaction Distractor percentage x Visual Field x Order of presentation, $F(2, 100) = 4.37$, $p = .015$, $\eta_p^2 = .08$ (see Fig. 39). Planned comparisons indicated that in the hard-easy order RTs were significantly slower in d67 than in the d33 in the RVF, $F(1, 50) = 4.48$, $p = .039$, $\eta_p^2 = .08$, as well as in the LVF, $F(1, 50) = 19.27$, $p < .001$, $\eta_p^2 = .28$. In the easy-hard order there was a trend towards faster RTs in d67 than in d33 in the RVF, $F(1, 50) = 3.81$, $p = .057$, $\eta_p^2 = .07$, but the difference between d67 and d33 in the LVF was not significant, $F(1, 50) = 0.48$, $p = .494$. The comparisons also revealed that RTs were significantly slower in d67 for LVF targets when participants began with the hard condition than when they began with the easy condition, $F(1, 50) = 4.53$, $p = .038$, $\eta_p^2 = .08$, although the order of presentation for RVF targets in d67 was not significant, $F(1, 50) = 1.65$, $p = .204$.

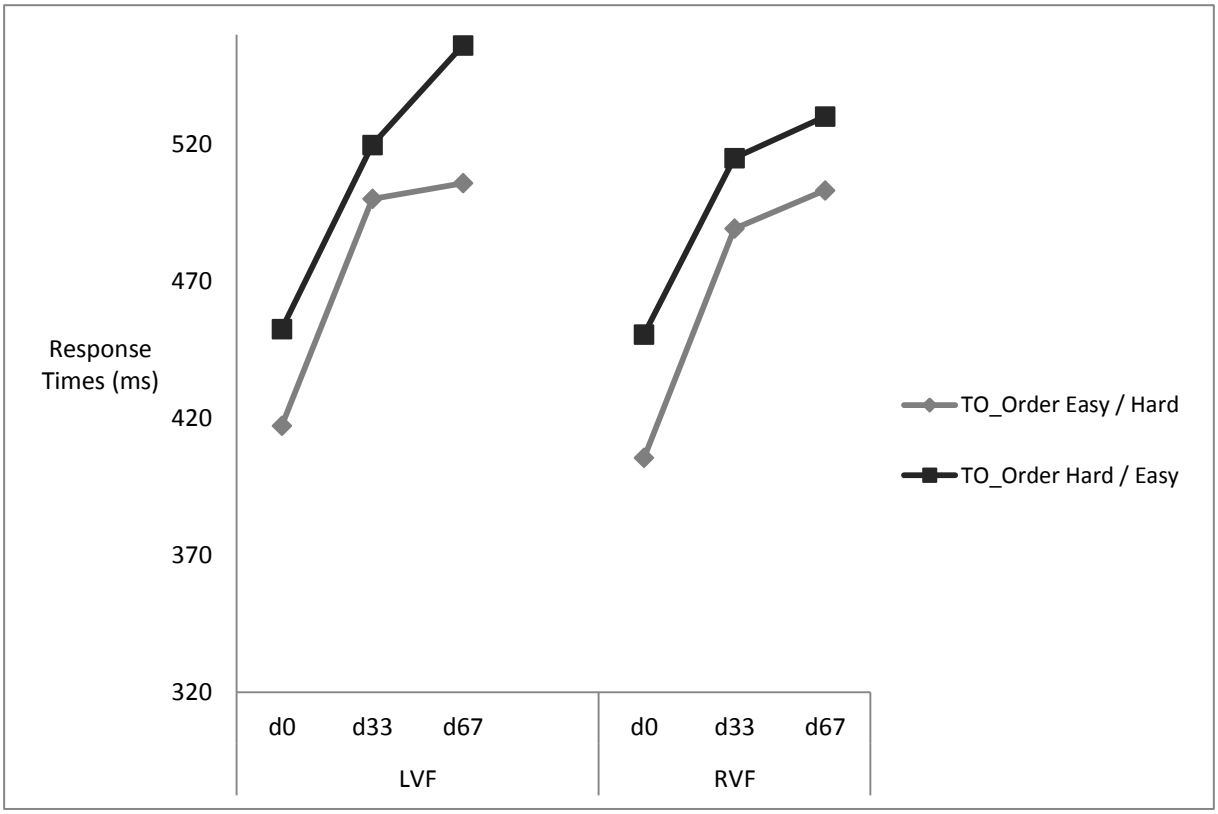

Figure 39: Mean response times in milliseconds (ms) to target-only trials (TO) in the left visual field (LVF) and in the right visual field (RVF) for each order of presentation (Easy/Hard, Hard/Easy) in Experiment 7.

We carried out an ANOVA on the slope values with visual field (LVF, RVF), and difficulty (easy, hard) as within subjects' factors and order of presentation (easy-hard, hard-easy) as between subjects' factor. There was an effect of difficulty, $F(1, 50) = 7.01$, $p = .011$, $\eta_p^2 = .12$, indicating that the distractor percentage had a smaller effect in the easy (1.1, *SD* = 0.72) than in the hard condition (1.41, *SD* = 1.09). The interaction Visual field x Order of presentation was significant, $F(1, 50) = 4.51$, $p = .039$, $\eta_p^2 = .08$. Planned comparisons revealed that this interaction was due to a smaller effect of distractor percentage in the RVF compared to the LVF when participants started by the hard condition, $F(1, 50) = 4.8$, $p = .033$, $\eta_p^2 = .09$, and no significant visual field difference when participants started by the easy condition, $F(1, 50) = 0.66$, $p = .421$.

Table 7

Mean response times in milliseconds and standard deviations (in parentheses) in Experiment 7 for target-only trials (TO) and target-following-distractor trials (TFD), as a function of the order of presentation (easy/hard [E-H], hard-easy [H-E]), the difficulty (easy, hard) and the visual field (LVF,RVF), in each block of trials (d0, d33, d67).

			TO			TFD	
Order	Difficulty	VF	d0	d33	d67	d33	d67
E-H	Easy	LVF	403 (93)	481 (90)	481 (87)	457 (87)	430 (79)
		RVF	397 (85)	472 (70)	481 (72)	451 (93)	426 (83)
	Hard	LVF	431 (94)	519 (103)	530 (101)	478 (105)	451 (102)
		RVF	415 (92)	507 (97)	525 (91)	440 (111)	442 (93)
H-E	Easy	LVF	448 (80)	501 (69)	525 (86)	459 (88)	449 (68)
		RVF	444 (78)	502 (69)	513 (82)	454 (68)	441 (75)
	Hard	LVF	457 (106)	539 (84)	587 (107)	519 (95)	502 (101)
		RVF	457 (96)	528 (78)	547 (95)	498 (95)	482 (69)

TFD trials

Repeated measures ANOVA were calculated on mean RTs, with distractor percentage (33% or d33, 67% or d67) visual field (LVF, RVF), and difficulty (easy, hard) as within subjects' factors, and order of presentation (easy-hard, hard-easy) as between subjects' factor. Mean RTs on TFD trials are shown in Figure 40. See Table 7 for the complete RTs data.

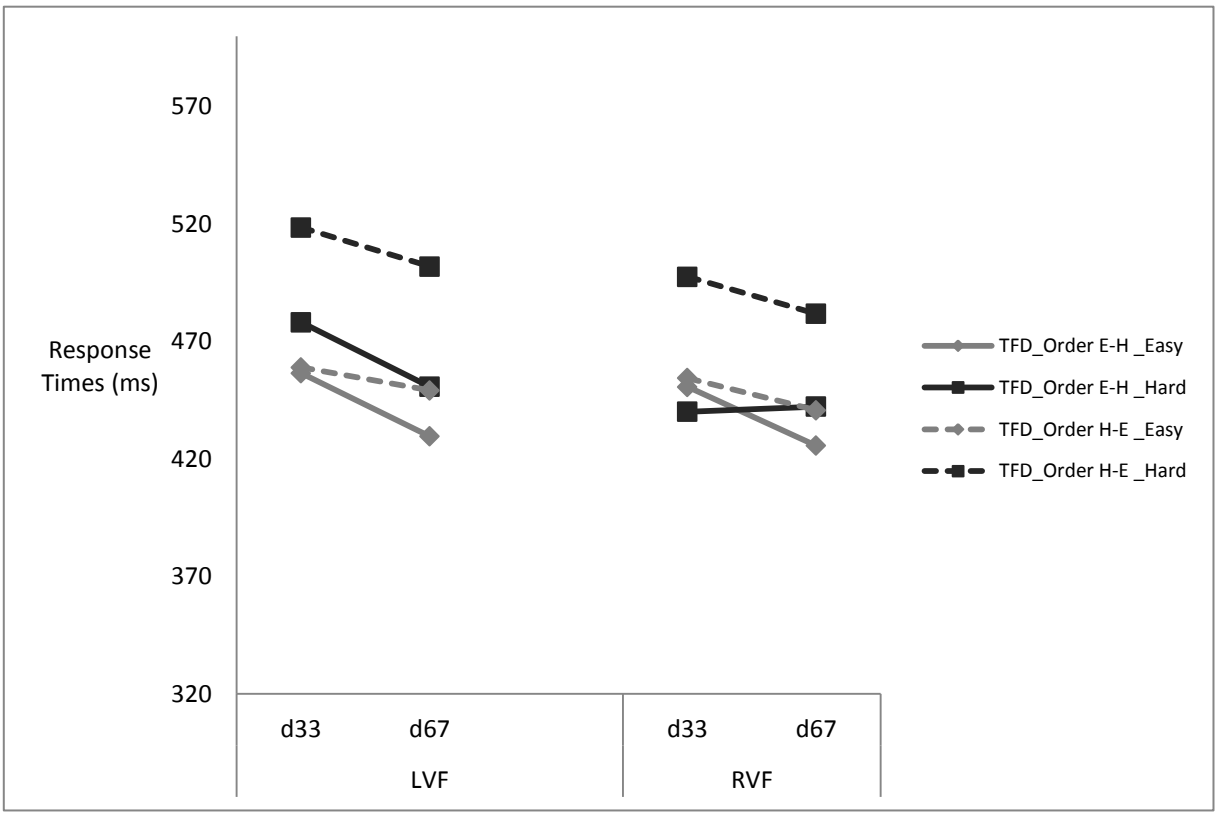

Figure 40: Mean response times in milliseconds (ms) to target-following-distractor trials (TFD) on the Easy and Hard conditions for each order of presentation (Easy/Hard [E-H], Hard/Easy [H-E]) in the left visual field (LVF) and in the right visual field (RVF) in Experiment 7.

There was an effect of difficulty, $F(1, 50) = 24.13$, $p < .001$, $\eta_p^2 = .33$, with faster RTs in the easy (446 ms, *SD* = 80) than in the hard condition (476 ms, *SD* = 99). There was an effect of distractor percentage, $F(1, 50) = 24.37$, $p < .001$, $\eta_p^2 = .33$, with faster RTs in d67 (453 ms, *SD* = 87) than in d33 (469 ms, *SD* = 95). There was also an effect of visual field, $F(1, 50) = 10.71$, $p = .002$, $\eta_p^2 = .18$, with faster RTs in the RVF (454 ms, *SD* = 88) than in the LVF (468 ms, *SD* = 94).

The interaction Visual field x Difficulty was significant, $F(1, 50) = 4.83$, $p = .033$, $\eta_p^2 = .09$. Planned comparisons indicated faster RTs for RVF (465 ms, *SD* = 95) than for LVF targets (487 ms, *SD* = 103) in the hard condition, $F(1, 50) = 12.9$, $p = .001$, $\eta_p^2 = .21$, but this difference was not significant in the easy condition, $F(1, 50) = 1.27$, $p = .265$.

The interaction Difficulty x Order was significant, $F(1, 50) = 8.74$, $p = .005$, $\eta_p^2 = .15$. Planned comparisons indicated slower RTs in the hard condition (500 ms, *SD* = 91) compared to the easy condition (451 ms, *SD* = 74) only when participants started by the hard condition,

$F(1, 50) = 30.95$, $p < .001$, $\eta_p^2 = .38$, but there was no significant difference when participants started by the easy condition, $F(1, 50) = 1.91$, $p = .173$.

Error data

We also measured the number of omissions and false alarms corresponding to each condition. For the easy condition the mean percentage of omissions was 0.32%, and the mean percentage of false alarms was 0.29%. For the hard condition the mean percentage of omissions was 1.37%, and the mean percentage of false alarms was 0.58%. As the frequency of errors was negligible for both conditions, no further analysis was carried out with these data.

8.4. Discussion

The goal of the present study was to examine the influence of the perceptual difficulty to discriminate targets from distractors on the hemispheric modulation of PA. The perceptual difficulty was given by the proximity of targets and distractors spatial locations. The results of Experiment 7 for targets appearing alone within a trial (TO) indicated faster RTs in the easy than in the hard condition. This finding is consistent with the proposal that increasing stimuli spatial proximity increases the difficulty to select the relevant target information (Eriksen & St. James, 1986). The stimuli perceptual difficulty interacted with the percentage of distractors. RTs to the target increased gradually as the probability of distractors increased in the hard condition. However, in the easy condition, RTs increased between the blocks without and with distractors (d0 and d33), but not between the two blocks containing distractors (d33 and d67). This finding suggests that PA directed to the target location was affected by the probability of distractors in the hard condition more than in the easy condition, suggesting that the effect of distracting events is inversely related to their proximity to the target. The proximity of targets and distractors in the hard condition may amplify the competition of the distractor with the target for PA.

For TO trials, there was also a main effect of visual field with faster RTs in the RVF than in the LVF. More importantly, this visual field advantage differed in relation to the task perceptual difficulty. Whereas there were faster RTs in the RVF than in the LVF in the hard condition, there was no visual field difference in the easy condition. This finding suggests a

LH advantage in preparation to RVF targets when stimuli spatial locations are harder to discriminate, consistent with studies showing a LH involvement in difficult situations in which the selection of target information is more difficult to achieve (e.g. Michael & Ojéda, 2005; Zhang et al., 2004). The visual field of presentation and the task perceptual difficulty did not interact with the percentage of distractors, contrary to our predictions. However, interestingly, there was a triple interaction between order of presentation, visual field and distractor percentage. The analyses of RTs data, suggest that this interaction is explained by a different pattern of responses in the LVF depending on the order of presentation. LVF RTs gradually increased between d33 and d67 when participants began with the hard condition, but not when they began with the easy condition. Consistent with RTs data, there was a larger slope of RTs as a function of distractor percentage in the LVF than in the RVF only when participants began with the hard condition.

A possible explanation of the interaction including the order is that practice and difficulty effects may have interacted. The stimulus repetition may have increased the familiarity of the target location, facilitating further target processing in that location (Risko, Stolz, & Besner, 2011), only in the easy context. The RH was associated with the recognition of objects in which subject have a lot expertise, and thus familiarity (Gauthier, Skudlarski, Gore, & Anderson, 2000; Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999). A familiarity (repetition) effect in the RH may have facilitated the target processing in the hard condition when beginning with the easy condition. In other words, increasing the target spatial location familiarity might have decreased the difficulty for the RH in recognizing the target from distractors in the hard condition, explaining why LVF RTs in the d67 block were faster in the easy-hard than the hard-easy order. The RH was presumably able to direct higher amounts of PA to the LVF target in the hard condition when preceded by the easy condition, counteracting the effect of distractors probability. These findings might also be associated with the RH sensitivity to the predictability of events in spatial and temporal dimensions. It can be argued that the RH was able to maximize the allocation of PA, only when the spatial uncertainty of a target was smaller as a consequence of stimulus familiarity. In contrast, the stimuli spatial uncertainty may activate the LH to develop a suitable preparatory strategy when subjects started by the hard condition, reducing the RH control in PA. More importantly, our findings also suggest that the hemispheric strategies used to modulate PA were independent of the processing taking place at the motor level, as in both conditions subjects performed the same task (location task).

After the appearance of a distractor within a trial, subjects only expect for the target to occur. In TFD trials, the distractor is not a competitor for PA, but it may act as a “reset” signal or a cue indicating that the target is about to appear. In Experiment 7, there were several findings in TFD trials. First, there was a main effect of distractor percentage, indicating that RTs were faster in the block with 67% than in the block with 33% of distractors. Increasing the probability of a distractor within a trial may also increase its cueing strength, because targets appear more frequently after a distractor.

Second, there were slower RTs in the hard condition than in the easy condition. A possibility is that using the distractor as a cue was more difficult when its perceptual discrimination from the target was hard. The difficulty to discriminate the target in TFD interacted with the order of presentation. RTs were slower in the hard than in the easy condition only when subjects began with the hard condition. When subjects began with the easy condition there was not a significant difference in RTs between the easy and the hard conditions. A strong possibility is that the difficulty to use the distractor as a cue in the hard condition was reduced when subjects began with the easy condition, owing to a relative facilitation in processing information at the target location after this location got familiar due to stimulus repetition (familiarity).

Finally, RTs for TFD trials were faster in the RVF than in the LVF. The advantage of RVF in TFD trials might be explained by the LH involvement in processing the distractor as a warning cue. Interestingly, the RVF advantage was only present in the hard condition. In the easy condition there was no visual field advantage. This finding suggests that the LH might be superior to the RH in using the distractor as a warning cue, especially when the perceptual discrimination between the target and the distractor stimuli is hard.

LH advantage in processing parts of an object

In the LAPT version used in the present study targets and distractors are located inside a rectangle. It can be argued that the RVF advantage obtained in Experiment 7 is the consequence of a LH specialization in allocating attention to a visual stimulus that corresponds to a part of an object (Arrington et al., 2000). The LH might have a special role in modulating PA when the expected stimuli are perceive as parts of an object. However, if the RVF advantage found in this study was due to a LH specialization in processing parts of an object we should have obtained the same pattern of responses for the easy and hard conditions

as in both conditions stimuli appeared inside a rectangle. This alternative hypothesis can be ruled out, owing to a different pattern of responses depending on the difficulty to discriminate the target from the distractor spatial locations in each condition.

LH advantage in processing categorical spatial relations

Another possibility is that the LH was recruited in Experiment 7 due to the categorical spatial representations needed to distinguish targets (small black square in the center of the rectangle) from distractors (small black square shifted above or below from the center rectangle). The LH is involved in spatial tasks in which subjects has to make categorical judgments about stimuli spatial relations, such as “above”, “bellow”, “in the middle” (Kosslyn, 1987; Kosslyn et al., 1989). This type of spatial representation may be used when the processing of spatial information is relatively easy. When judgments about the spatial relation between stimuli are more difficult, another type of spatial representation is used to represent precise distances and locations, that is a coordinate spatial representation, which is computed faster in the RH (Parrot, Doyon, Démonet, & Cardebat, 1999). However, according to this proposal, we should have obtained a RVF advantage only in the easy condition and a LVF advantage in the hard condition. Our results showed a RVF advantage in the hard condition and no specific visual field advantage in the easy condition.

8.5. Conclusion

The findings of the present study suggest that the task perceptual difficulty affected in a different manner the modulation of PA in each visual field, thus in each hemisphere. When the discrimination of a target location from distractor location is hard, given their spatial proximity, the LH may be particularly recruited to develop a strategy to modulate the intensity of PA directed to upcoming events (*frequency matching* strategy). When the perceptual discrimination between targets and distractors becomes easier, the RH might be able to develop a suitable preparatory strategy according to events probabilities in space and time (*maximizing* strategy). Hemispheric strategies to modulate PA might take place at the perceptual level of processing, being independent of the processing taking place at the motor programing level.

GENERAL DISCUSSION AND CONCLUSION

The main goal of this thesis was to examine the role of each brain hemisphere in the modulation of PA to a spatial location. We tested two different hypotheses. The first hypothesis suggests that only the RH controls PA to a spatial location in the visual field (RH hypothesis). A second hypothesis suggests that both hemispheres participate in PA to a spatial location, each hemisphere being differentially involved in the modulation of PA (DH hypothesis). To test the hemispheric involvement in PA, we developed a lateralized version of the APT (LaBerge et al., 2000), the LAPT, in which targets were presented in RVF or LVF, thus are first processed by the LH or the RH, respectively (divided visual field paradigm). We developed several versions of the LAPT in which the distractors were presented in the center of the display (Experiments 1-5) or lateralized (Experiments 6 and 7). In all LAPT versions, the probability of the distractor varied in three successive blocks. The increase of the expected distractor probability is assumed to increase the amount of PA directed to it prior to its occurrence. Consequently, relatively less PA is directed to the target location, increasing RTs. In the LAPT as in the APT, distractors never appeared simultaneously with the target, and a target may follow a distractor or not in a trial. We were particularly interested in RTs to the target when a distractor did not actually appear but was simply expected to occur, in each of the successive blocks. In these trials with a target alone, subjects presumably form expectations for distracting stimuli, particularly in the block where they often occur before the target onset. Thus, the LAPT allows the evaluation of the influence of the distractor expectation on the intensity of PA directed to the target location in each visual field/hemisphere, while the distractor is actually not present.

Our results show that the modulation of PA directed to a lateralized target when the expectation of a distracting stimulus increased was different in the RVF and the LVF. The visual field differences may be the consequence of different processing strategies in each hemisphere, in agreement with the DH hypothesis. These strategies are presumably related to the differential processing of the information arising from the probability of events. According to our findings these strategies might take place at the perceptual level of information processing rather than at the motor programming level. Our results also suggest that one processing strategy can apply to the whole visual field when one hemisphere is

dominant in a specific situation. When both hemispheres are in conflict for the development of different strategies, visual field differences occur. Some aspects of the task seemed to have a critical role in the development of each hemispheric strategy. In the next sections, we will review and discuss the main findings obtained in this thesis with regard to the modulation of PA in each visual field/hemisphere. We will propose an interpretation of our results in the frame of the theoretical accounts of the triangular circuit theory of attention (LaBerge, 1995, 1997, 2002). Finally, we will draw some conclusions and future perspectives.

9.1. The modulation of PA in the LH

The LH was shown to be sensitive to the expected probability of target and distractor stimuli. RTs for RVF targets increased gradually as the probability of a distractor appearance increased. We proposed that the LH modulates PA by taking into account the probability of possible events. The LH may use a *frequency matching* strategy to modulate PA, based on the actual frequency of past events (Wolford et al., 2000). This strategy was related to the LH involvement in probability learning (Kincses et al., 2004), and the advanced information about the probability of events may accelerate the strategic use of these probabilities to control PA (Chapter 4 and 5). Several authors associated the *frequency matching* strategy with the human capacity of searching for causal relations in the sequence of events and the ability of generating complex rules to guide behavior under uncertainty (Burns & Demaree, 2009; Unturbe & Corominas, 2007; Yellott, 1969). The *frequency matching* observed in our experiments might be related to the distribution of PA resources in an uncertain context.

The LH might modulate PA specifically when there is some uncertainty about the spatio-temporal characteristics of an expected event. Consistent with this proposal, the uncertainty about the target appearance in spatial (Chapter 8) and temporal (Chapter 5) dimensions seemed to increase the LH involvement in the control of PA. The task may be perceived as more difficult when the uncertainty about the relevant target event appearance increases. In Chapter 8, we found that the LH was presumably involved in modulating PA to a target when the proximity between the locations of the target and the distractor overlapped. In Chapter 5, the temporal proximity between delays in which target and distractor stimuli could occur might also influenced the LH involvement in PA. It was argued that increasing the proximity of events in temporal and spatial dimensions in our experiments increased the difficulty to select the relevant target from irrelevant distractors. These results suggest that the

LH is especially recruited to modulate PA in difficult tasks. In attentional demanding tasks, the LH might enhance attentional activity directed to the target location and reduce the activity directed to distractor locations in preparation to their occurrence (Chapter 7). Our findings are in agreement with studies suggesting the LH implication in the development of a preparatory strategy when the attentional demands of the task are high (Luks et al., 2007; MacDonald et al., 2000).

Thus, taking together these findings, the LH might modulate PA in complex or difficult tasks by distributing attentional resources as a function of the expected probability of the different events (see Fig. 41).

9.2. The modulation of PA in the RH

The RH was shown to be sensitive to the higher probability of occurrence of the target stimulus in time. Our results showed that RTs to targets in the LVF differed depending on the temporal predictability of the target. RTs in the LVF were affected by the mere presence or absence of distractors, but not their frequency when the delay of the target was highly predictable (Chapters 4 and 6). In contrast, RTs in the LVF were affected by the distractors probability when the delay of a target's appearance was uncertain (Chapter 5). We proposed that the RH modulates PA to a spatial location according to the target temporal predictability. The RH may use a *maximizing* strategy (Wolford et al., 2000) to modulate PA, consisting in maximize the enhancement of PA directed to the target at the time interval in which the target occurrence was highly predictable. However, when this strategy is rendered difficult, the LH *frequency matching* strategy applies to the whole visual field (Chapter 5).

The RH might also be capable of *maximizing* PA to the target when the spatial location of the target is well separated from the distractor location. The RH may develop a suitable preparatory strategy when the perceptual discrimination of events is relatively easy, owing to the high spatial predictability of the target (Chapter 4 and 6). In contrast, increasing the perceptual difficulty to discriminate targets from distractors affected the *maximizing* strategy (Chapter 8). Precisely, RTs in the LVF were influenced by the frequency of distractors when the spatial location where the target could appear overlapped with the spatial location where the distractor could occur. In such a condition, the stimuli spatial uncertainty might certainly reduce the spatial predictability of the target, affecting the RH preparatory

strategy. Interestingly, the effect of distractors in the LVF under perceptual difficulty decreased when subjects started by a task in which stimuli spatial locations was relatively easy to distinguish. This finding suggests that the RH might be able to develop its preparatory strategy as the spatial certainty of events increased due to a familiarity effect.

Taking together our results, the RH might modulate PA in relatively easy tasks by allocating attentional resources to events with higher probability or certainty in spatio-temporal dimensions (see Fig. 41).

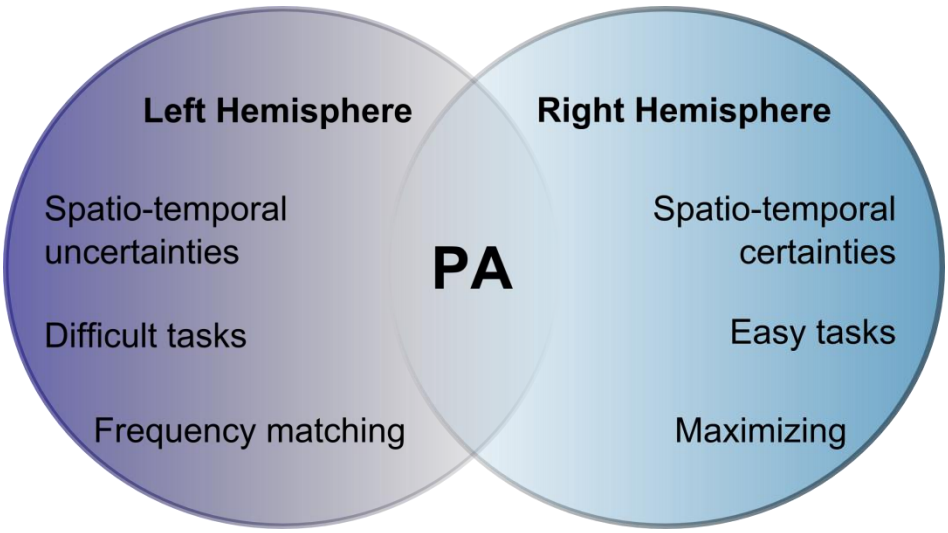

Figure 41: Schematic representation of the differential hemispheric hypothesis in PA. Both hemispheres may develop complementary strategies to modulate PA in different situations.

9.3. Alternative hypotheses to explain visual field/hemispheric differences

9.3.1. *Automatic activation of neuronal pathways by events repetition*

An alternative explanation to the RVF pattern of result is the automatic preactivation of neuronal networks when the repetition of specific trials increases (Lamb, London, Pond, & Whitt, 1998). If the number of trials containing a distractor is high, like in d67, the neuronal network processing distractor stimuli would be more activated, and the occurrence of a rare event (TO trials) would produce slower RTs. The RVF/LH might therefore be affected by repetition rather than by a frequency matching strategy. In our experiments, there were

actually four types of trials (blank; target-alone; target-following-distractor; distractor-alone) and no specific type of trials appeared with a frequency superior to 37.5%. Consequently, repetition was rare. Moreover, the automatic activation of neuronal pathways by events repetition cannot explain why the effect of the distractor probability depends on the instruction (explicit *vs* implicit instruction on the distractor probability) or why the effect is mainly found in the RVF. Thus, we believe that a *frequency matching* strategy of PA by the LH is more plausible.

9.3.2. *Events rate and alertness*

An alternative explanation to the lack of difference in RTs between the two blocks of trials containing distractors for LVF targets in some experiments is the increase in the level of vigilance or intrinsic alertness between blocks. The RH was shown to be greatly involved in vigilance tasks (Posner & Petersen, 1990; Posner, 2008; Warm, Matthews, & Parasuraman, 2009), and increasing the stimulus rate improves performance in these tasks, with faster RTs (Jenkins, 1958; Parasuraman & Davies, 1976). In the LAPT, the number of distractors increases progressively between blocks. As the total number of targets does not vary, this means that the global number of possible events also increases between blocks. The increase in events rate possibly increases the level of vigilance or intrinsic alertness in the RH, and this vigilance increase may counteract the effects of the increased probability of distractors in d67 when compared with d33. However, the number of events increased in the three blocks of trials for all the experiments presented her. For instance, there was always 60 and 84 possible events (without the “practice” trials) in d33 and d67 blocks respectively whichever the experiment. The “counteracting” effect of alertness cannot explain why LVF RTs increased between d33 and d67 blocks in Experiments 3 and 7. Therefore, the *maximizing* strategy of PA in the RH is a more plausible explanation to the lack of difference in RTs between d33 and d67 obtained in some experiments of this thesis.

9.4. Hemispheric differences in the triangular-circuit of attention?

In the theoretical assumptions of the triangular-circuit theory, the intensity of attentional activity directed to a particular location is regulated by the frequency to which a task-relevant signal appeared in that location (LaBerge et al., 2000). This regulation would

occur in frontal regions of the brain. However, the theoretical accounts of the triangular-circuit theory do not differentiate attentional operations in the RH and the LH, suggesting that the thalamocortical circuits of both hemispheres are capable of producing PA in a similar fashion.

According to the data presented in this thesis, PA directed to a spatial location differs between visual fields, and thus between hemispheres. Our findings suggest that the selective and modulatory control of attention in the frontal cortex of the LH and the RH might be different. This hemispheric difference may rely on the way that each hemisphere processed the information arising from the frequency of events. Thus, there might be two modes of information processing in PA localized in the LH and the RH, respectively. Each of these modes may intervene in different situations.

The RH may modulate PA to a spatial location when the target signal is easy to distinguish from distracting noise. The RH may increase the intensity of PA directed to a spatial location of well-differentiated objects. The RH might only enhance activity to a target location when this location is well separated from a distractor location (Chapters 4 and 6). Interestingly, the separation of objects in time was also critical for the RH modulatory process. Increasing the proximity of distracting events in spatial and time dimensions seemed to affect the modulation of PA in the RH (Chapters 5 and 8). One possibility is that the selective control module localized in the RH is only able to process highly predictable information in space and time (e.g. Vallesi & Crescentini, 2011). The RH selective control may develop a strategy consisting in enhancing attention toward the target at the location and delay in which its occurrence is highly predictable. The RH may presumably control PA in the whole visual field when the target and distractors are easy to discriminate.

The LH may be particularly recruited to develop a preparatory strategy when the discrimination of the signal from noise is more difficult to achieve due to spatial and temporal uncertainty. The LH might be especially involved in the control of PA when the information arising from sensory pathways is harder to discriminate. Under perceptual difficulty, the selective control module located in the LH might develop a suitable preparatory strategy to distribute PA in the whole visual field. The modulation of PA may presumably interact between hemispheres in difficult tasks because the LH was demonstrated to be capable to control attention only in the RVF (Corbetta, Miezin, Shulman, & Petersen, 1993; Heilman & Valenstein, 1979; Mesulam, 1981; Perry & Zeki, 2000). A possibility is that the modulatory control of the LH that receives the information generated in the ipsilateral selective control

area may transfer this information, presumably via de fibers of the corpus callosum, to the modulatory control area located in the RH (see Fig. 27). As a consequence, the pattern of responses is similar in both visual fields because the LVF and the RVF inputs are both presumptively modulated by the strategy developed in the selective control area located in the LH.

In summary, the data obtained in this thesis suggest some modifications in the triangular-circuit theory proposed by LaBerge et al. (2000). Both hemispheres might be capable of modulating the intensity of attentional activity directed to a spatial location prior to a target occurrence in that location. However, each hemisphere may differ in the strategy used in this modulatory process. Additionally, our results open a possible distinction of intra- *vs* inter-hemispheric pathways in the triangular circuit of attention. More specifically, a question is whether the transfer of PA strategy between hemispheres via the corpus callosum occurs in anterior (frontal) or posterior (parietal) regions when one hemisphere applies its own strategy to the whole visual field. Further research should be necessary to examine in more detail the characteristics of each pathway.

9.5. Hemispheric differences in PA or perceptual bias?

The visual field differences found in the present study may be also related to environmental factors known to produce perceptual bias. Environmental factors, such as habits in reading direction or hand preference, demonstrated to play a role in the way humans behave in the different parts of the space, thus in the different parts of the visual field. These factors may modulate the cognitive processing of spatial and temporal information.

9.5.1. *Handedness and bias in visual perception*

The dominance in the use of the left or the right hand has been shown to influence human performance in certain tasks. The visual field asymmetries in the processing of information depend on the dominant hand of individuals. For instance, normal right-handers have a bias to identify a half-face presented in the LVF, but not the left-handers (Levy, Heller, Banich, & Burton, 1983).

In the present thesis, the participants of the experimental studies were all strongly right handed. It may be possible that the hand preference also influenced the modulation of attention in each visual field. In dextrals, the left hand performs more rigid and regular movements (e.g., hold a cup to serve tea, hold a flask to open it, etc.) while the right hand usually makes more variable and detailed ones (e.g. writing, drawing, using the computer mouse, etc.). These asymmetries in motor processing might also influence visual perception. Future research should address this issue, comparing the modulatory control of PA in each visual field between subjects with opposite hand preference.

9.5.2. *Reading habits and bias in visual perception*

Reading habits has also been demonstrated to be an influential factor in the utilization of space. Changing the reading direction changes the scanning direction in the visual field. Reading and writing direction habits are from right to left in English, French or Spanish but from left to right in Hebrew, Arabic or Urdu. The reading habits were shown to influence the representation of time and space. For instance, Chokron and Imbert (1993) examined the effect of reading habits in the performance of a spatial task. Authors asked subjects with opposite reading direction habits to mark the middle of a horizontal line placed in a median position. A leftward bias in this task has been generally reported for right-handed subjects, and explained by the over-activation of the RH due to the spatial nature of the task (Bowers & Heilman, 1980). However, Chokron and Imbert found an asymmetrical perceptual bias relative to scanning habits. Whereas subjects with right-to-left reading habits deviated to the right of the middle, subjects with left-to-right reading habits deviated to the left. Reading scanning habits may influence biases in preparatory attention, due to the competition between hemispheres (see Siéroff, Dahmen, & Fagard, 2012). Recently, other experiments demonstrated that there is a bias in the spatial representation of time depending on the directional reading habits (Ouellet, Santiago, Funes, & Lupiáñez, 2010; Ouellet, Santiago, Israeli, & Gabay, 2010). The results of these studies suggest that reading habits direction is an important factor in the study of perceptual asymmetries.

In the present thesis, most participants had a left-to-right reading direction habit. It may be possible that reading direction has a role in the perceptual asymmetries found in our experiments. This issue should be addressed in future studies by comparing the modulatory control of PA in each visual field between subjects with opposite reading habits direction.

9.6. Conclusion and perspectives

The aim of this thesis was to examine the role of each brain hemisphere in the modulation of PA to a spatial location. The results obtained in several experiments suggest that the modulation of PA differs in the LVF and the RVF. These visual field differences were related to hemispheric differences in the modulation of PA towards a target and distractor locations. We proposed that each hemisphere uses a different strategy to regulate the intensity of PA directed to a spatial location. These strategies were associated with stimuli expected probability and they were intrinsically related to the difficulty to select the relevant stimulus for further processing. The LH might be specially recruited to develop a preparatory strategy in selective complex situations, when the target stimulus is more difficult to discriminate from the distractor stimulus, whether in the temporal or the spatial dimensions. The LH might use a *frequency matching* strategy to modulate PA that consists in matching the allocation of attentional activity prior to the target occurrence with the expected probability of targets and distractors. The RH may develop a preparatory strategy when targets are easy to discriminate from distractors, given their predictability or certainty in space and time. The RH might use a *maximizing* strategy to modulate PA that consists in enhancing the intensity of PA to the target location at the time interval in which the target is highly predictable.

The data presented in this thesis suggest that normal adults do not prepare in the same manner in both visual fields. This finding might have relevant implications in the performance of tasks requiring attentional preparation in the entire visual field. For instance, a goalkeeper and a tennis player might differ in their strategic preparation in each visual field during penalty kicks and service, respectively. In rugby, attacks and defense on the left and the right space of the field intrinsically differ. However, visual field differences may occur in much more frequent situations like driving, eating at lunch, or even processing dynamic faces from the left or the right side (Arnold, Bécue, & Siéroff, in press; Siéroff, 2001). Future studies addressing preparatory processes in these daily situations might provide useful information, and with more ecological validity, about the strategies used to allocate attention across the visual field.

The visual field differences found in this thesis were obtained using behavioral measurements in normal population. Other methodological approaches in neuroscience were shown to be useful tools to study hemispheric differences in information processing. Future research using other methods may clarify some aspects of the modulation of PA by the brain

hemispheres. For instance, electrophysiological recordings should give us information about the time course of PA in each hemisphere. Imaging studies could be useful to specify the brain areas involved in the preparatory processes under different situations. Most importantly, research on patients with lateralized neural damage on frontal areas might provide relevant information about the capacity of the intact hemisphere in the modulation of PA as well as the consequence of the lesion on preparatory behavior. Hence, the use of other methods in neuroscience should increase our knowledge on the involvement of each hemisphere in PA, complementing the findings presented in this thesis.

Résumé de thèse (french)

L'Attention Préparatoire (AP) permet d'anticiper la survenue imminente d'un événement. Par exemple, une personne attendant un bus qui doit arriver d'une minute à l'autre se prépare à voir le bus. Lors de cette préparation, la personne se forme une représentation mentale (image mentale) des caractéristiques du bus (taille, numéro, couleur) et maintient cette représentation mentale pour détecter l'arrivée du bus le plus rapidement et le plus efficacement possible. C'est grâce à la représentation mentale du bus que l'attention rehausse l'activation des régions cérébrales impliquées dans la perception visuelle du bus (en quelque sorte une préperception).

L'AP est la capacité de moduler (rehausser) l'intensité de l'attention dirigée vers un stimulus avant son apparition, en empêchant que le sujet soit distrait par une information non pertinente. Différents facteurs interviendraient dans la modulation de l'AP, notamment la fréquence d'apparition du stimulus. Un réseau neuronal formé de différentes régions corticales et sous-corticales seraient impliquées dans l'AP (LaBerge, 1995, 1997). Ce réseau neuronal serait constitué des aires frontales impliquées dans le contrôle attentionnel, et connectées aux aires plus postérieures impliquées dans le traitement sensoriel. Selon certaines études, la modulation de l'AP dépendrait de l'hémisphère droit (HD), c'est l'hypothèse unilatérale, et selon d'autres études, la modulation de l'AP dépendrait des deux hémisphères, l'hémisphère gauche (HG) et l'HD qui interviendraient selon des stratégies différentes, c'est l'hypothèse différentielle. L'objectif principal de cette thèse est de tester ces deux hypothèses en étudiant le rôle joué par chaque hémisphère dans la modulation de l'AP dirigée vers une localisation de l'espace.

LaBerge, Auclair et Siéroff (2000) ont développé un paradigme simple pour évaluer la modulation de l'intensité de l'AP dirigée vers une localisation de l'espace, l'APT (pour *Attentional Preparation Test*). Les auteurs ont fait varier lors de plusieurs blocs d'essais la probabilité d'apparition d'un stimulus dans une localisation. Ils ont montré que la fréquence relative d'apparition d'un stimulus dans une localisation de l'espace modulait l'AP dirigée vers cette localisation. Lors de ce travail de thèse, nous avons développé différentes versions de l'APT afin d'évaluer la capacité de chaque hémisphère à allouer de l'AP dans une localisation de l'espace. Nous avons utilisé la méthode de présentation des stimuli en champ

visuel divisé (présentation d'un stimulus dans le champ visuel gauche, CVG, ou dans le champ visuel droit, CVD), selon laquelle les performances à une tâche donnée sont meilleures dans le champ visuel opposé à l'hémisphère spécialisé dans cette tâche. Les voies visuelles étant croisées dans le cerveau, un stimulus présenté dans le CVG est d'abord traité par l'HD et un stimulus présenté dans le CVD est d'abord traité par l'HG. Par conséquent, les différences de performance observées entre les champs visuels, par exemple lors d'une tâche attentionnelle, seraient la traduction de différences de fonctionnement attentionnel entre chaque hémisphère.

Nous avons mené une série de cinq études expérimentales dans le but de tester la capacité de chaque hémisphère à moduler l'AP dirigé dans une localisation de l'espace. D'une part, ces études nous ont permis d'évaluer le mode de traitement de chaque hémisphère impliqué dans la modulation de l'AP. D'autre part, ces études nous ont permis de cibler les différents facteurs impliqués dans la modulation de l'AP. Ces études sont en faveur de l'hypothèse d'une implication différente de chaque hémisphère dans l'AP.

Etude 1 : Effet de la probabilité d'un distracteur dans la modulation de l'AP par les hémisphères cérébraux

La probabilité d'apparition d'un stimulus dans l'espace est un des facteurs déterminant de l'intensité de l'AP dirigée vers ce stimulus (LaBerge et al., 2000). Par exemple, lorsque la probabilité d'un stimulus cible augmente, l'intensité de l'AP dirigée vers la cible augmente. Si un distracteur apparait lors de la phase de préparation précédant l'apparition de la cible, il peut entrer en compétition avec la cible pour l'AP. Par conséquent, l'augmentation de la probabilité d'apparition d'un distracteur diminuerait l'intensité relative d'attention dirigée vers la cible avant son apparition, ce qui augmenterait les temps de réponse (TR) à la cible. La modulation de l'AP dirigée vers la cible et /ou le distracteur est donc un processus dynamique qui serait influencé par la probabilité d'apparition des stimulus lors d'une tâche donnée. L'objectif de cette première étude était d'évaluer la capacité de chaque hémisphère à moduler l'AP.

Dans la littérature, il n'y a pas consensus autour du rôle tenu par chaque hémisphère dans la modulation de l'AP. Selon une première hypothèse, la modulation de l'AP dépendrait de l'HD (hypothèse unilatérale). Différentes études ont rapporté l'activation de plusieurs

régions dans l'HD au moment de la préparation à la perception d'un stimulus visuel, suggérant que l'HD serait spécialisé dans la modulation de l'AP (Brunia et Damen, 1988; Brunia et al, 2000). Selon une deuxième hypothèse, les deux hémisphères seraient impliqués dans la modulation de l'AP, mais d'une manière différente (hypothèse différentielle). L'implication de chaque hémisphère dans la modulation de l'AP serait liée à la manière dont chacun des hémisphères traite l'information provenant de la probabilité des événements.

L'HD serait particulièrement engagé lors du traitement d'un stimulus visuel ayant une grande régularité et une grande prédictibilité dans l'espace et dans le temps (Coull et coll., 2000; Vallesi et al., 2008; Vallesi & Crescentini, 2011). Le rôle spécifique de l'HD dans le traitement des stimulus hautement probables pourrait être lié à la stratégie utilisée par cet hémisphère lors de l'anticipation des stimulus ayant des probabilités différentes. Lors d'une tâche dans laquelle il faut prédire quel stimulus apparaîtra parmi deux stimulus dont les probabilités d'apparition sont différentes, la stratégie de l'HD consiste à choisir systématiquement le stimulus qui était plus fréquent dans le passé (Wolford et al., 2000). Cette stratégie de « maximisation » pourrait être basée sur un processus de préparation au stimulus le plus fréquent et le plus prédictible. Ainsi, la modulation de l'AP par l'HD serait associée au traitement de stimulus hautement prédictibles : des stimulus avec une forte probabilité d'apparition spatiale et temporelle.

L'HG utiliserait une stratégie différente de celle de l'HD pour anticiper l'apparition des stimulus ayant des probabilités différentes d'apparition. L'HG choisirait les stimulus en fonction de leur fréquence dans le passé, ce qui signifie qu'il utiliserait une stratégie d'adaptation à la fréquence des événements (*frequency matching strategy* ; Wolford et al., 2000). La stratégie utilisée par l'HG, lorsque il anticipe des stimulus dans le futur, pourrait être liée à une implication plus générale de cet hémisphère dans l'apprentissage des probabilités (Kincses et al., 2004). L'HG utiliserait l'information accumulée à partir de la fréquence d'apparition des stimulus pour distribuer les ressources attentionnelles sur ces stimulus en fonction de leur probabilité d'apparition (Hecht et al., 2010; Robertson et al., 1988). Ainsi, L'HG serait également impliqué dans la modulation de l'AP, mais il utiliserait une stratégie différente de l'HD.

Afin de tester l'implication de chaque hémisphère dans la modulation de l'AP, nous avons développé une version latéralisée du APT (LaBerge, Auclair & Siéroff, 2000), le LAPT (pour *Lateralized Attentional Preparation Test*). Dans le LAPT, la cible apparaît dans le CVG ou dans le CVD et le distracteur apparaît au centre de l'écran. La probabilité d'apparition du

distracteur varie dans trois blocs d'essais consécutifs avec 0% (d0), 33% (d33) et 67% (d67) de distracteurs. Les différences de performances entre le CVG et le CVD en fonction de la probabilité d'apparition de la cible nous donnent des indications sur les stratégies de traitement de deux hémisphères (HG/CVD *vs* HD/CVG).

Nous avons évalué la modulation de l'AP dans chaque hémisphère en fonction de la probabilité d'apparition des distracteurs. Nous nous sommes intéressés en particulier aux réponses des essais ne comportant pas de distracteur (essais cible seule) pour évaluer l'AP. Dans ces essais, l'attente d'un distracteur entrerait en compétition avec l'attente de la cible pour l'AP, influençant l'intensité d'attention dirigée vers la cible avant son apparition. Nous avons examiné les temps de réponses aux cibles apparaissant dans le CVD et dans le CVG, ce qui nous donne une mesure de l'intensité de l'AP dans l'HG et l'HD respectivement.

Afin de tester nos hypothèses, nous avons conduit deux expériences avec le LAPT en variant la tâche du sujet. Dans l'Expérience 1, nous avons utilisé une tâche de localisation dans laquelle l'hémisphère qui perçoit la cible contrôle également la réponse à la cible. Les sujets devaient répondre avec la main gauche quand la cible était dans le CVG, et avec la main droite quand la cible était dans le CVD. Cependant, l'HG serait plus impliqué que l'HD dans une tâche impliquant plusieurs réponses possibles, comme c'est le cas de la tâche de localisation (Rushworth et al., 1997; Schluter et al., 2001, 1998). Dans le but de minimiser l'activation de l'HG par la tâche, nous avons utilisé une tâche de détection, avec une seule réponse possible, dans l'Expérience 2. La main de réponse était contrebalancée entre les sujets. Les participants ont été informés de manière explicite (consigne explicite) sur la proportion d'apparition des distracteurs avant chaque bloc d'essais. La probabilité temporelle de la cible était constante entre les différents blocs d'essais. Plus précisément, lorsque la cible apparaissait dans un essai, elle apparaissait toujours vers la fin de l'essai (délais longs). Par conséquent, le délai d'apparition de la cible dans un essai était hautement prédictible. Le distracteur, quant à lui, apparaissait dans des délais plus courts, antérieurs à la présentation de la cible (délais courts).

Si la modulation attentionnelle permettant de rehausser le traitement d'un stimulus sélectionné dépend de l'HD (hypothèse unilatérale), nous devrions trouver des temps de réponse (TR) plus rapides et une moins grande sensibilité au distracteur pour les cibles du CVG par rapport à celles du CVD. En d'autres termes, nous nous attendons à observer une pente des TR en fonction du nombre de distracteurs plus faible quand la cible apparaît dans le CVG que quand elle apparaît dans le CVD. Si chaque hémisphère à une stratégie qui lui est

propre pour moduler l'AP sur une cible (hypothèse différentielle), nous devrions trouver un pattern de résultats différent dans le CVG et le CVD avec des stratégies d'attente distinctes pour chaque hémisphère. L'HG baserait sa stratégie d'attente sur la fréquence des cibles et des distracteurs (stratégie d'adaptation à la fréquence des événements). Du fait que seule la fréquence des distracteurs varie dans les différents blocs d'essais, nous devrions obtenir une augmentation graduelle des TR en fonction de la probabilité d'apparition des distracteurs dans le CVD. L'HD baserait sa stratégie d'attente sur la haute prédictibilité de l'apparition de la cible dans un essai (stratégie de maximisation). Nous devrions obtenir des TR aux cibles plutôt réguliers dans le CVG en raison de la haute prédictibilité de la cible lors des longs délais. Concernant la tâche à effectuer, nous nous attendons à un avantage des TR aux cibles dans le CVD / HG lors de la tâche de localisation.

Les résultats de ces expériences ont montré un effet global du pourcentage de distracteurs, interagissant avec le champ visuel, en accord avec l'hypothèse différentielle. En particulier, nous avons trouvé une augmentation graduelle des TR pour la cible dans le CVD lorsque le pourcentage de distracteurs augmente. Ce résultat suggère que l'HG (contrôlant le CVD) serait sensible à la probabilité exacte d'apparition d'un distracteur, surtout si cette probabilité a été explicite dans la consigne. L'HG utiliserait une stratégie d'adaptation à la fréquence des événements pour moduler l'intensité de l'AP vers une cible. Par ailleurs, avec la tâche de localisation nous avons trouvé un avantage du CVD dans certains blocs d'essais. Ce résultat suggère une implication de l'HG lors d'une tâche dans laquelle les sujets doivent choisir entre plusieurs réponses, comme c'est le cas de la tâche de localisation, avantage qui s'annule lorsqu'une seule réponse est requise (tâche de détection).

Pour les cibles présentées dans le CVG, les TR augmentaient entre les blocs d'essais sans et avec distracteurs, mais il n'y avait pas de différence de TR entre les deux blocs contenant des distracteurs (d33 et d67). L'HD, contrôlant le CVG, serait sensible à l'apparition d'un distracteur, mais maintiendrait un niveau d'AP vers une cible indépendamment de la probabilité exacte de l'apparition du distracteur. Ces résultats seraient liés au rôle de l'HD dans la préparation à l'apparition d'un stimulus quand celui-ci est très prédictible. Dans le LAPT, l'apparition d'une cible à la fin d'un essai est plus probable que l'apparition d'un distracteur à la fin d'un essai. L'HD utiliserait une stratégie de maximisation pour moduler l'AP allouée à la cible. Cette stratégie consisterait à rehausser systématiquement la préparation à la cible à la fin d'un essai. La prédictibilité temporelle de la cible jouerait

donc un rôle fondamental dans le développement de la stratégie de maximisation développée par l'HD.

Le pattern de résultats obtenu dans chaque champ visuel ne serait pas lié au niveau moteur du processus. En effet, les résultats ne dépendent pas de la main de réponse lors de la tâche de détection. Cela suggère que les différentes stratégies utilisées par l'HG et l'HD pour moduler l'intensité de l'AP se mettent en place à un niveau perceptif du traitement de l'information.

En conclusion, les résultats obtenus dans cette première étude sont en accord avec l'hypothèse différentielle qui stipule que chaque hémisphère utilise une stratégie différente pour moduler l'intensité de l'AP allouée à une cible.

Etude 2 : Effet de la probabilité temporelle d'un stimulus sur la modulation hémisphérique de l'AP

L'intensité de l'AP dirigée vers une localisation de l'espace avant l'apparition d'un stimulus cible dans cette localisation serait influencée par le délai de l'apparition de cette cible. Certaines études suggèrent que le traitement d'une cible est plus rapide et plus efficace lorsque notre attention est dirigée vers le moment d'apparition de cette cible (e.g. Coull et al., 2000). Lorsque le délai d'apparition de la cible est variable, la réponse à la cible est plus rapide au moment auquel la cible a la plus forte probabilité d'apparaître (Niemi & Näätänen, 1981; Trillenberg et al., 2000). La probabilité temporelle d'apparition d'une cible est bénéfique pour le comportement du sujet car elle provoquerait un rehaussement stratégique de l'attention au moment le plus prédictible de l'apparition de la cible. Ainsi, la probabilité temporelle des stimulus jouerait un rôle fondamental dans la modulation stratégique de l'intensité de l'AP. Le but de cette deuxième étude est d'examiner l'influence de la probabilité temporelle d'apparition d'un stimulus cible sur la modulation hémisphérique de l'AP.

La probabilité temporelle d'une cible serait déterminante pour la modulation de l'intensité de l'AP dans l'HD (Coull et al., 2000; Vallesi et al., 2009). Les résultats de notre étude précédente suggèrent que la prédictibilité de la cible dans des délais longs jouerait un rôle fondamental dans le développement d'une stratégie de maximisation par l'HD. En

revanche, la probabilité temporelle de la cible n'aurait pas d'influence particulière sur la stratégie d'adaptation à la fréquence des événements, développée par l'HG.

Pour tester ces hypothèses, nous avons conduit une expérience en utilisant une version du LAPT dans laquelle nous avons manipulé la probabilité temporelle d'apparition de la cible. La probabilité d'apparition des distracteurs augmentait selon trois blocs d'essais consécutifs (d0, d33, et d67), comme dans les Expériences 1 et 2. Contrairement aux Expériences 1 et 2, dans l'Expérience 3, la cible pouvait apparaître lors de délais courts ou longs. Par conséquent, la prédictibilité du moment d'apparition de la cible dans un essai était plus faible que dans nos expériences précédentes. Le distracteur pouvait apparaitre uniquement lors de délais courts, comme dans nos expériences précédentes. Ainsi, même si la cible et le distracteur n'étaient jamais présentés simultanément, le moment auquel le distracteur pouvait apparaitre pouvait coïncider avec le moment auquel la cible pouvait apparaitre.

Si la stratégie de maximisation utilisée par l'HD pour moduler l'intensité de l'AP dirigée vers une cible était liée à la prédictibilité temporelle de la cible, elle devrait être affectée par la manipulation de la prédictibilité temporelle de l'apparition de la cible. D'autre part, si la stratégie d'adaptation à la fréquence des événements, utilisée par l'HG pour moduler l'AP, était liée à la fréquence attendue des stimulus plutôt qu'au moment auquel ils peuvent apparaitre, elle ne devrait pas être influencée par la manipulation de la prédictibilité temporelle de l'apparition de la cible.

Nos résultats ont montré une augmentation des TR lorsque la probabilité d'apparition du distracteur augmente, comme dans notre première étude. Cette augmentation était graduelle dans le CVD, comme dans les Expériences 1 et 2, mais aussi dans le CVG, contrairement aux Expériences 1 et 2. Ces résultats suggèrent que l'HD n'a pas pu développé sa stratégie de maximisation dans l'Expérience 3, à cause de l'incertitude temporelle de l'apparition de la cible. Ces résultats sont en accord avec l'hypothèse du rôle fondamental de la probabilité temporelle d'un stimulus cible pour la modulation de l'AP dans l'HD.

La difficulté de l'HD pour développer sa stratégie d'attente renforcerait le contrôle de l'HG sur l'AP. Ce renforcement résulterait en une mise en place d'une stratégie d'adaptation à la fréquence des évènements dans tout le champ visuel. Le pattern de résultats similaire dans les deux champs visuels pourrait donc être expliqué par le renforcement de l'HG.

En conclusion, les résultats de cette deuxième étude suggèrent que la modulation de l'AP par l'HD serait sensible à la probabilité temporelle d'apparition de la cible. L'incertitude

temporelle de l'apparition de la cible empêcherait l'HD de maximiser le rehaussement vers la cible avant son apparition. Le contrôle de l'HG dans la modulation de l'AP serait renforcé par le contexte d'incertitude temporelle dans lequel les stimulus apparaissent ainsi que par la difficulté de l'HD à développer une stratégie préparatoire. Le renforcement de l'activation de l'HG aboutirait à une application de la stratégie d'adaptation à la fréquence des événements à l'ensemble du champ visuel.

Etude 3 : L'apprentissage implicite de la probabilité d'un stimulus et la modulation hémisphérique de l'AP

L'intensité de l'activité attentionnelle dirigée vers un stimulus avant son apparition est modulée par sa probabilité. La probabilité d'un stimulus peut être indiquée explicitement par avance aux participants ou elle peut être apprise implicitement par les participants à partir de la séquence des événements. Le but de cette troisième étude était d'examiner la modulation de l'AP par chaque hémisphère lorsque l'augmentation de la probabilité d'apparition des distracteurs est apprise à partir de la séquence des événements.

Dans nos études précédentes, les réponses dans le CVD montraient un pattern d'adaptation à la fréquence des événements. Nous voulions examiner si ce résultat dépendait d'un processus automatique ou plutôt d'un processus contrôlé mis en place par l'HG. Selon une première hypothèse, l'augmentation de TR en fonction de la probabilité d'apparition des distracteurs dans le CVD dépendrait d'un processus automatique. L'HG calculerait la fréquence des événements de manière automatique à partir de la séquence des événements (Lamb et al., 1998; Risko et al., 2008). Selon une deuxième hypothèse, le pattern d'adaptation à la fréquence des événements pour les cibles dans le CVD dépendrait d'un processus contrôlé. L'HG utiliserait l'information sur la probabilité d'apparition des stimuli de manière stratégique afin de distribuer l'intensité de l'AP sur chaque stimulus en fonction de sa probabilité. Dans nos Expériences 1-3, les participants étaient informés de manière explicite (consigne explicite) avant chaque bloc d'essais quant à la probabilité approximative d'apparition des distracteurs. L'anticipation de la proportion d'apparition des distracteurs dans un bloc d'essais pourrait permettre à l'HG de se préparer stratégiquement à l'apparition des événements. Cette information serait un facteur déterminante du développement d'une stratégie préparatoire d'adaptation à la fréquence des événements par l'HG (Luks et al., 2007;

MacDonald et al., 2000). Par ailleurs, la stratégie de maximisation de l'HD pourrait aussi être renforcée par l'information explicite sur la proportion d'apparition des distracteurs (Fantino & Estefarandi, 2002).

Afin de tester nos hypothèses nous avons mené deux expériences (Expériences 4 et 5) dans lesquelles l'information sur la proportion d'apparition des distracteurs avant chaque bloc d'essais était absente (consigne implicite). L'apparition temporelle de la cible dans un essai était hautement prédictible, comme dans les Expériences 1 et 2. Dans l'Expérience 4, nous avons utilisé une tâche de détection, dans laquelle les deux hémisphères seraient impliqués de manière égale. Nos résultats précédents ont montré une implication plus importante de l'HG dans une tâche plus complexe (tâche de localisation, Expériences 1 et 3), avec plusieurs réponses alternatives. Nous voulions évaluer si la performance d'une tâche plus complexe pouvait suffire à activer la stratégie préparatoire de l'HG. A cette fin, nous avons utilisé une tâche de localisation dans l'Expérience 5.

Si le pattern d'adaptation à la fréquence des événements trouvé dans nos expériences précédentes est lié à un calcul automatique de la fréquence des événements par l'HG, nous devrions trouver un pattern de résultats similaire pour les cibles dans le CVD, aussi bien avec la tâche de détection (Expérience 4) qu'avec la tâche de localisation (Expérience 5). En revanche, si le pattern de réponses d'adaptation à la fréquence des événements est associé à un processus contrôlé de distribution stratégique de l'AP, cette stratégie devrait être affectée par l'absence d'information sur la proportion d'apparition des distracteurs avant chaque bloc d'essais. De plus, si la stratégie préparatoire de l'HG peut se déclenchée par la simple complexité de la tâche, activant l'HG, nous devrions trouver un pattern de réponses d'adaptation à la fréquence des événements dans le CVD uniquement avec une tâche de localisation (Expérience 5). Par ailleurs, si la consigne explicite renforce la stratégie de maximisation de l'HD, cette stratégie devrait être perturbée par une consigne implicite.

Nos résultats ont montré que le pattern de réponses était différent avec une consigne implicite par rapport à une consigne explicite. Cependant, cette différence n'a été trouvée que pour les réponses dans le CVD/HG. Pour les cibles dans le CVG/HD le pattern de réponses était similaire à celui obtenu avec une consigne explicite. Les TR à la cible augmentaient en fonction de l'absence ou présence d'un distracteur (différence entre d0 et d33), mais les TR étaient semblables pour les deux blocs contenants des distracteurs (absence de différence de TRs entre d33 et d67). Ce résultat suggère que la consigne explicite ne jouerait pas un rôle important sur le développement de la stratégie préparatoire de l'HD.

Dans les deux expériences avec consigne implicite le pattern de réponses à la cible dans le CVD/HG était similaire au pattern de réponses obtenu dans le CVG/HD, contrairement aux expériences semblables avec une consigne explicite (Expériences 1 et 2). En particulier, les TR étaient affectés par la présence d'un distracteur dans un bloc, mais pas par sa fréquence. Ce résultat suggère que le pattern de réponses obtenu dans le CVD lors de nos études précédentes serait lié à des processus contrôlés mis en place par l'HG, plutôt qu'à des processus de calcul automatique des fréquences. Dans nos études précédentes, l'information sur la proportion d'apparition des distracteurs avant chaque bloc d'essais jouerait un rôle fondamental dans la formation d'une stratégie d'adaptation à la fréquence des événements par l'HG. De plus, nos résultats ont montré que la complexité de la tâche ne peut pas déclencher à elle seule cette stratégie dans l'HG.

Le contrôle de l'HD sur l'AP serait renforcé par la prédictibilité de la cible ainsi que par la difficulté de l'HG à développer sa stratégie préparatoire. Ce renforcement résulterait en une mise en place d'une stratégie de maximisation dans tout le champ visuel. Le pattern de résultats similaire dans les deux champs visuels pourrait donc être expliqué par le renforcement de l'HD.

En conclusion, les résultats de cette troisième étude soutiennent l'hypothèse du rôle fondamental de la prédictibilité ou certitude temporelle d'apparition de la cible pour le développement d'une stratégie de *maximisation* par l'HD. D'autre part, nos résultats suggèrent que le pattern d'adaptation à la fréquence des événements serait le résultat de la mise en place d'un processus stratégique contrôlé par l'HG.

Etude 4 : Effet du renforcement de l'attention par une consigne sur la modulation hémisphérique de l'AP

L'intensité de l'AP dirigée vers une localisation spatiale peut être renforcée de manière volontaire. Le renforcement de l'intensité de l'attention dirigée vers la localisation d'une cible augmenterait la rapidité et l'efficacité de son traitement et diminuerait les effets des distracteurs (LaBerge et al., 2000). Le but de cette quatrième étude était de tester la capacité de chaque hémisphère à renforcer l'intensité de l'AP dirigée vers la localisation d'une cible au moyen d'une consigne.

LaBerge et al. (2000) ont montré que les participants pouvaient renforcer volontairement leur préparation attentionnelle en faveur de la cible grâce à une simple consigne. Ils ont utilisé deux consignes induisant une attention faible (consigne faible) ou une attention forte (consigne forte) vers la cible. Ils ont montré qu'avec une consigne forte le sujet renforçait son attention vers la cible et diminuait l'attention dirigée vers les distracteurs. Le renforcement de l'attention dirigée vers la cible avec la consigne forte entraînait des TR plus courts et une diminution de l'effet de la probabilité d'apparition des distracteurs par rapport à une consigne faible.

L'HG serait spécialement impliqué dans le renforcement de l'attention dirigée vers une cible. L'HG a été associé au rehaussement stratégique vers une cible après une consigne indiquant que la sélection d'une cible parmi des distracteurs demanderait plus d'effort attentionnel (Luks et al., 2007; MacDonald et al., 2000). L'HG rehausserait l'attention vers la cible en préparation à son apparition. En plus de ce processus de rehaussement, l'HG réduirait l'activité provenant des distracteurs afin de diminuer leur interférence sur la performance du sujet (Zhang et al., 2004). Ainsi, l'HG serait impliqué dans le renforcement de l'AP vers une cible et dans la réduction de l'activité dirigée vers les distracteurs lors d'une tâche demandant plus d'effort attentionnel.

Afin de tester la capacité de chaque hémisphère dans le renforcement de l'intensité de l'AP vers une cible, nous avons comparé des TR à la cible lorsque le participant dirigeait une attention forte ou faible vers la cible. Comme dans l'étude de LaBerge et al., (2000), nous avons utilisé une consigne faible pour induire une attention faible sur la cible, et une consigne forte pour induire une attention forte sur la cible. Lors d'une consigne faible, il était mentionné aux participants qu'ils devaient répondre à la cible mais pas aux distracteurs. Dans ce cas, ils dirigeaient leur attention vers la cible mais aussi vers les distracteurs. Lors d'une consigne forte, il était mentionné aux participants qu'ils devaient se concentrer uniquement sur la localisation de la cible. Dans ce cas, les sujets dirigeraient leur attention uniquement vers la cible.

Le renforcement de l'intensité de l'AP vers la localisation de la cible plutôt que vers la localisation du distracteur requerrait deux processus distincts : le rehaussement de l'attention dirigée vers la cible et la réduction de l'activité attentionnelle dirigée vers le distracteur. Nous voulions tester l'implication de chaque hémisphère dans ces deux processus. Pour cela, nous avons comparé les performances des sujets dans deux versions du LAPT, différentes par la localisation du distracteur. Dans une des versions, le distracteur était central (comme dans les

Expériences 1-5), tandis que dans l'autre version le distracteur était latéral. Lorsque le distracteur est central la réduction de l'activité attentionnelle vers le distracteur serait partagée par les deux hémisphères. En revanche, lorsque le distracteur est latéral cette réduction serait d'abord réalisée par l'hémisphère controlatéral.

Si l'HG est impliqué dans le renforcement de l'attention dirigée vers la cible par une consigne ainsi que dans la réduction de l'activité dirigée vers le distracteur, nous devrions obtenir, avec une consigne forte, des TR plus rapides et moins d'effet de la probabilité d'apparition d'un distracteur pour les cibles dans le CVD, aussi bien avec un distracteur central qu'avec un distracteur latéral.

Les résultats de cette expérience ont montré un effet global de la consigne interagissant avec le pourcentage de distracteurs. En particulier, nous avons trouvé des TR plus rapides et moins d'effet de la probabilité d'apparition des distracteurs avec une consigne forte, en accord avec notre hypothèse sur l'effet global de la consigne. Toutefois, contrairement à nos hypothèses, cet avantage de la consigne forte était présent pour les cibles dans le CVD comme dans le CVG. Ce résultat suggère que les deux hémisphères ont été impliqués dans le rehaussement de l'attention vers la cible avec la consigne.

De plus, avec une consigne forte nous avons obtenu des TR plus rapides dans le CVD que dans le CVG dans la version du LAPT avec distracteur latéral. L'HG pourrait être davantage impliqué que l'HD dans la réduction de l'attention dirigée vers le distracteur lors d'une tâche qui demande plus d'effort attentionnel.

En conclusion, les résultats de cette quatrième étude suggèrent que les deux hémisphères seraient capables de rehausser l'intensité de l'AP dirigée vers une cible au moyen d'une consigne. En plus de cette capacité de rehaussement, l'HG serait impliqué dans la réduction de l'activité attentionnelle dirigée vers le distracteur dans des tâches demandant plus de contrôle attentionnel.

Etude 5 : Effet de la difficulté perceptive sur la modulation de l'AP

L'AP permet de rehausser le traitement d'une cible, tout en résistant à l'interférence possible de distracteurs. L'influence d'un distracteur augmente lorsque sa proximité à la cible augmente (Eriksen & St. James, 1986). Quand les distracteurs sont proches de la cible,

l'attention allouée aux distracteurs perturberait le traitement de la cible. L'intensité de l'AP dirigée vers une cible serait donc influencée par la difficulté perceptive lors d'une tâche donnée. Le but de cette cinquième étude était d'évaluer l'influence de la difficulté perceptive, donnée par la proximité spatiale entre la cible est le distracteur, dans la modulation hémisphérique de l'AP.

Les résultats de nos études précédentes suggèrent que L'HD maximiserait le rehaussement de l'attention dirigée vers des stimulus très prédictibles (Brunia et al., 2000; Coull et al., 2000; Vallesi & Crescentini, 2011; Vallesi et al., 2008), avec une grande certitude dans l'espace et dans le temps. L'HD pourrait donc être impliqué dans la modulation de l'AP dirigée vers une cible lorsque sa localisation spatiale est très prédictible à condition qu'elle soit relativement facile à distinguer de celle du distracteur. En revanche, l'HG serait engagé dans la modulation de l'intensité de l'AP dirigée vers une cible quand sa sélection parmi des distracteurs est difficile à accomplir (Luks et al., 2007; MacDonald et al., 2000; Michael & Ojéda, 2005; Zhang et al., 2004). Il pourrait donc être impliqué quand la localisation de la cible est difficile à distinguer de celle du distracteur.

Afin de tester ces hypothèses, nous avons créé une version du LAPT manipulant la proximité spatiale entre la cible et le distracteur. Dans l'Expérience 7, nous avons comparé les performances des sujets dans deux conditions expérimentales. Dans la condition facile, la localisation spatiale de la cible était distincte de celle des distracteurs. Dans la condition difficile, la localisation spatiale dans laquelle le distracteur pouvait apparaitre se superposait en partie avec la localisation spatiale dans laquelle la cible pouvait apparaitre (même si la cible et le distracteur n'étaient jamais présentés simultanément). Le délai d'apparition de la cible était hautement prédictible. Nous avons utilisé une consigne implicite, afin de minimiser l'activation de la stratégie développée par l'HG par des facteurs autres que la difficulté perceptive de la tâche. Les sujets ont exécuté une tâche de localisation dans les deux conditions de l'Expérience 7.

Si la stratégie préparatoire développée par chaque hémisphère est liée à la difficulté perceptive de discriminer la cible du distracteur, nous devrions obtenir un pattern de réponses différent dans le CVD et le CVG en fonction de la condition expérimentale. Dans la condition facile, nous devrions obtenir un pattern de réponses similaire aux expériences lors desquelles la cible avait une haute prédictibilité spatiale et temporelle (Expériences 4 et 5). L'HD devrait être capable de maximiser l'AP dirigée vers la cible lors d'une condition facile dans laquelle la cible est hautement prédictible dans l'espace et dans le temps. Dans la condition difficile,

nous devrions trouver un pattern de réponses similaire à l'Expérience 3, dans laquelle il y avait une haute incertitude sur le moment d'apparition de la cible. L'incertitude spatiale de la cible dans la condition difficile devrait également activer l'HG avec sa stratégie d'adaptation à la fréquence des événements.

Nos résultats ont montré que la difficulté perceptive d'une tâche donnée affectait de manière différente la modulation de l'AP dans chaque champ visuel/hémisphère. Lorsque la discrimination des localisations de la cible et du distracteur est difficile, en raison de leur proximité spatiale, l'HG serait impliqué dans la modulation de l'intensité de l'AP dirigée vers le stimulus (stratégie d'adaptation à la fréquence des événements). Lorsque la discrimination perceptive entre la cible est le distracteur est plus facile, l'HD serait capable de développer une stratégie adaptée à la probabilité des stimulus dans l'espace et dans le temps (stratégie de maximisation). Toutefois, nos résultats indiquent que l'ordre des tâches joue aussi un rôle, avec une implication accrue de l'HG lorsque les participants commencent par la condition difficile et une implication accrue de l'HD lorsqu'ils commencent par la condition facile, quelle que soit la difficulté de la tâche. Cela indiquerait que la stratégie mise en place par un hémisphère s'imposerait dès la première condition (facile ou difficile) et resterait dominante par la suite.

Nos résultats suggèrent aussi que la stratégie utilisée pour moduler l'AP par chaque hémisphère serait indépendante des processus moteurs, car les participants ont effectué la même tâche (tâche de localisation) dans les deux conditions.

Conclusion

Le but de cette thèse était d'examiner le rôle de chaque hémisphère cérébral dans la modulation de l'intensité de l'AP dirigée vers une localisation spatiale. Les résultats obtenus dans plusieurs études expérimentales suggèrent que la modulation de l'AP serait différente dans le CVG et dans le CVD. Ces différences de champs visuels sont vraisemblablement liées aux différences hémisphériques dans la modulation de l'intensité de l'AP dirigée vers la localisation spatiale d'une cible et d'un distracteur. Chaque hémisphère utiliserait une stratégie différente pour réguler l'intensité de l'AP dirigée vers une localisation. Ces stratégies sont associées à la probabilité d'apparition d'un stimulus et seraient liées à la difficulté dans une tâche donnée pour sélectionner un stimulus cible parmi des stimulus distracteurs. L'HG

développerait une stratégie d'adaptation à la fréquence des événements pour moduler l'AP. Cette stratégie consisterait à distribuer l'intensité de l'AP sur la cible et le distracteur en fonction de leur probabilité d'apparition. L'HG serait principalement impliqué dans la modulation de l'AP lors des situations complexes de sélection, aussi bien dans l'espace que dans le temps. L'HD développerait une stratégie de maximisation pour moduler l'AP. Cette stratégie consisterait à rehausser l'intensité de l'AP dirigée vers la localisation de la cible au moment où elle est hautement prédictible. L'HD serait principalement impliqué dans la modulation de l'AP dans des situations où la discrimination de la cible est relativement facile, grâce à sa prédictibilité dans l'espace et dans le temps. En conclusion, les modèles de l'AP doivent tenir compte des différentes stratégies mises en place par l'hémisphère gauche et l'hémisphère droit. Ces stratégies sont parfois en compétition, et nous avons obtenu des résultats différents dans le CVD et le CVG dans plusieurs de nos expériences. Parfois, les résultats se ressemblent dans le CVD et le CVG, mais l'allure des RT en fonction du pourcentage des distracteurs indiquerait que l'un des deux hémisphères a « imposé » sa stratégie à tout le champ visuel.

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