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Differential hemispheric modulation of preparatory attention

Laura Gabriela Fernández, Eric Siéroff *

EA 4468 Equipe Neuropsychologie du vieillissement, Institut Paris Descartes de Psychologie, Paris Descartes University, Paris, France

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ABSTRACT

Preparatory attention (PA) is the ability to allocate attention to a stimulus prior to its occurrence and is a crucial component of attentional control. We investigated the role of brain hemispheres in PA using an experimental test in which normal participants responded to a target that could appear in the right or the left visual fields, thus projecting to the left or the right hemispheres, while ignoring a central distractor that could appear in the preparatory phase preceding the target. This experimental test measures the ability of participants to modulate PA directed to a target location when the probability of a distractor occurrence varies across three blocks of trials (0%, 33%, 67%). The competition between distractors and target for PA should produce slower response times when the probability of distractors is high. Three experiments were conducted varying the temporal predictability of the target occurrence within a trial (high predictability in Experiments 1 and 3, and low predictability in Experiment 2), and the task used (location in Experiments 1 and 2, and detection in Experiment 3). We found that the modulation of PA by the expected probability of events was different in each visual field/hemisphere. Whereas the left hemisphere PA was influenced by the mere probability of events in each block of trials, the right hemisphere PA was mainly influenced by events with high temporal predictability. These results suggest that each hemisphere uses a different strategy to modulate PA when directed to a target location at the perceptual level of visual processing.

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1. Introduction

A crucial aspect of attentional control is the anticipation of an upcoming stimulus. This anticipation should increase the speed and effectiveness both of processing the expected stimulus and the response. For instance, the expectation of a green traffic light speeds up the processing of the green color for a driver, taking him less time to accelerate. Preparatory attention (PA), the ability to allocate attention to a stimulus prior to its occurrence, may act by generating a mental representation of the expected stimulus, increasing the signal-to-noise ratio, and preventing observers from being distracted by interfering stimuli (LaBerge, 1995). PA, a prolonged aspect of attention, can be distinguished from selection, or brief attention (LaBerge, 1995). While selection is a rapid process, occurring in tens of ms, specifically involved when several stimuli have to be discriminated, preparation is a slower process, occurring over a range of seconds, involving an enhancement of attention to a particular stimulus before it is expected to occur. The expectation of a specific stimulus is highly dependent on the experience of similar stimuli in the past. It has been shown that PA is modulated by the relative frequency of the target and distractor stimuli in the past, thus by the predictability of different events (LaBerge, Auclair, & Siéroff, 2000). The modulation of PA directed to a target also depends on the timing of events, and more specifically to the predictability of a stimulus at a given point in time (Niemi & Näätänen, 1981; Trillenberg, Verleger, Wascher, Wauschkuhn, & Wessel, 2000).

PA may lead to the enhancement of brain activity in areas where a particular target stimulus is processed prior to its onset. Such enhancement may be controlled by prefrontal areas, as shown by imaging (Kastner, Pinsk, De Weerd, Desimone, & Ungerleider, 1999), electrophysiological (Padilla, Wood, Hale, & Knight, 2006), and patient studies (Auclair, Jambaqué, Dulac, LaBerge, & Siéroff, 2005; Barceló, Suwazono, & Knight, 2000; Rosahl & Knight, 1995; Siéroff et al., 2004). Several studies suggest that the prefrontal areas of right (RH) and left (LH) hemispheres make different contributions to attentional processing (Corbetta & Shulman, 2002; Posner & Petersen, 1990). However, there is no general agreement about whether there is hemispheric specialization in PA. A first hypothesis is that the RH plays a major role in PA (RH hypothesis). Using EEG recordings, Brunia and Damen (1988)

* Corresponding author. Address: Université Paris Descartes, EA 4468 Equipe Neuropsychologie du vieillissement, Centre Henri Piéron – Institut de Psychologie, 71, avenue Edouard-Vaillant, 92774 Boulogne-Billancourt Cedex, France.

E-mail address: eric.sieroff@parisdescartes.fr (E. Siéroff).

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measured the stimulus preceding negativity (SPN) prior to the onset of an expected feedback stimulus that did not require any response from observers. The SPN reflects the anticipatory attention for the upcoming stimulus and is part of the contingent negative variation (CNV), considered to be an index of preparation processes (Brunia & van Boxtel, 2001). Brunia and Damen (1988) found larger activity in the RH and concluded that the RH plays an important role in allocating PA to a delayed perceptual stimulus. As well, a PET study found an activation of the prefrontal cortex (PFC), insula, and parietal cortex of the RH when anticipating a stimulus (Brunia, de Jong, van den Berg-Lenssen, & Paans, 2000).

The RH involvement in preparation of an expected stimulus has been shown using different methods in patients with unilateral frontal damage (Picton, Stuss, Shallice, Alexander, & Gillingham, 2006; Stuss et al., 2005; Vallesi et al., 2007) and in a normal population (Vallesi, McIntosh, Shallice, & Stuss, 2008). The anticipation of a perceptual stimulus may involve the estimation of the time interval at which this stimulus occurs. The RH might be essential in this estimation of time intervals (Lewis & Miall, 2006), especially with intervals as long as seconds (Jones, Rosenkranz, Rothwell, & Jahanshahi, 2004). When targets can occur at different time intervals within a trial, responses are faster at the most probable interval, i.e. when the target is highly predictable (Niemi & Näätänen, 1981; Trillenberg et al., 2000). This behavioral benefit has been related to the enhancement of attentional activity in preparation to the target appearance. Frontal areas of the RH are specifically involved in the enhancement of attention at time intervals at which the target is highly predictable (Coull, Frith, Büchel, & Nobre, 2000; Vallesi et al., 2008). The sensitivity of the RH to the most predictable event has also been shown in a study in which split-brain patients and patients with unilateral frontal damage had to guess the forthcoming occurrence of two possible stimuli with different probabilities. The RH of two split-brain patients and one patient with left frontal damage used a *maximizing* strategy based on the systematic prediction of the most frequent stimulus (Wolford, Miller, & Gazzaniga, 2000). Hence, according to these studies, PA to an expected stimulus might be lateralized to the RH, and this preparation might be modulated by highly predictable events, particularly when these events occur with high temporal probability.

In addition to the implication of the RH in PA, several findings suggest that the LH might also be able to allocate attentional resources prior to the presentation of a stimulus in some situations. Two attention-related functions of the LH might be important in PA: selection control, which is necessary in complex situations, and interpretation of past events. The first function, selection, is related to the attentional demands of the task. By testing patients with unilateral posterior damage, Rushworth, Nixon, Renowden, Wade, and Passingham (1997) found that the LH is implicated in tasks that involve making a choice, so-called choice reaction time (RT) tasks, although both hemispheres are involved in simple RT tasks. Similar results have been found with TMS (Schluter, Rushworth, Passingham, & Mills, 1998) and PET (Schluter, Krams, Rushworth, & Passingham, 2001) methods, suggesting that the LH may play a role in response selection. Posner and Petersen (1990) suggested that anterior areas of the LH control the allocation of visual attention, when signal selection is necessary. Furthermore, when the upcoming attentional demands of a task are informed in advance, different LH regions are activated. It has been suggested that these regions are crucial for the selection and the deployment of a preparatory strategy in order to recruit attentional resources (Luks, Simpson, Dale, & Hough, 2007; MacDonald, Cohen, Stenger, & Carter, 2000).

The second role that the LH may play in PA is related to the influence of past events' frequency. Wolford et al. (2000) have shown that a patient's LH uses a specific strategy when it must guess the occurrence of two possible stimuli with different probabilities. Unlike the RH, the LH bases its guesses on the frequency of each stimulus that occurred in the past, a strategy known as *frequency matching*. For instance, if the frequency of a red square and a green square were 80% and 20%, respectively, the LH would guess a red square in about 80% of the trials and a green square in about 20% of the trials. Therefore, the *frequency matching* strategy consists of guessing, or predicting, future events based on the frequency of those events in recent past. This strategy might be related to the LH capacity for actively interpreting reality under uncertainty (Wolford, Newman, Miller, & Wig, 2004; Wolford et al., 2000). It can be argued that, when guessing the next event in the near future, participants may induce a preparatory state before the stimulus arrival, controlling the allocation of PA to one stimulus or the other. Thus, the results of these studies suggest that the LH plays a role in the PA to upcoming events, taking into account the relative frequency of these events in the past.

In summary, there are two different hypotheses concerning the role of brain hemispheres in PA. The first hypothesis is that the RH is specialized in PA processes (RH hypothesis). However, PA may not be exclusively lateralized to the RH, and a second hypothesis is that both hemispheres are involved in the modulation of PA, using different strategies (Differential Hemispheric hypothesis, DH). The RH strategy might be related to the high temporal predictability of events (e.g. occurring at a predictable delay), and the LH strategy might be related to the relative frequency of the different events in recent past. The aim of the present study was to test these two hypotheses.

In order to examine the role of each hemisphere in PA to a visual location, we developed a lateralized version of the method proposed by LaBerge et al. (2000), a simple test of PA, we call the Attentional Preparation Test (APT). 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 an observer expects a target stimulus, it might compete for the allocation of PA. When the probability of the distracting stimulus is high, relatively less PA should be allocated to the target, increasing RT. In the APT, three empty boxes were displayed horizontally on the screen at the beginning of each trial, as a warning signal. Then, the target was presented as a black square in the central box, appearing after a variable delay of approximately 2 seconds. A distractor, a black square in one of the lateral boxes, could also appear at a delay of approximately 1 second. Thus, the distractor occurred in the preparatory phase preceding the occurrence of the target. These long delays were used because PA is a slow process taking at least 1 or 2 seconds to develop, according to ERP studies (Jennings & van der Molen, 2005; LaBerge, 2005). In order to minimize selective attention effects, the target never appeared simultaneously with the distractor, and the three boxes were sufficiently separated in space to reduce errors to a negligible level. The frequency of trials containing a distractor varied in several blocks. It was reasoned that increasing the probability of a distractor stimulus before the target would increase the intensity of attentional activity directed to the distractor location. As a consequence, relatively less attentional activity would be directed to the target location, increasing the RT to the target. Indeed, the results of this experiment showed a linear increase in the RTs to the target as a function of the probability of distractor trials. These findings from the study using the APT showed that the observers' PA for the occurrence of targets as well as distractors was modulated by their appearance in recent trials. Hence, the amount of attentional activity directed to a stimulus prior to its onset is assumed to be a continuously variable modulation process, and we aimed to study whether this modulation differs in the two brain hemispheres.

We developed a lateralized version of the APT, called the LAPT (for Lateralized Attentional Preparation Test), using the divided

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