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Vertical asymmetries and inhibition of return: Effects of spatial and non-spatial cueing on behavior and visual ERPs



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ABSTRACT

The mechanisms underlying inhibition of return (IOR) are still under debate. Besides the probable implication of several processes in its generation, a reason for this uncertainty may be related to experimental factors affecting the presence, time course, and magnitude of IOR. Two of them may be related to the arrangement of the stimuli in the visual field that could cause possible interactions between IOR and response conflict effects (horizontal arrangements) or between IOR and perceptual asymmetries (vertical arrangement). The purpose of the present study was to explore location and color cueing effects with a vertical arrangement of stimuli, free of S–R compatibility effects. To examine this possibility, a cue-back task with stimuli in the vertical meridian was employed. Targets could randomly and equiprobably appear at cued or uncued locations, or with cued or uncued color. These cueing effects were analyzed on behavior and ERPs separately for upper and lower visual fields (UVF and LVF). Under location cueing, behavioral responses were slower (spatial IOR) in both hemifields. In the ERPs, N1 reductions were observed in both visual fields although with different modulations in their latency and scalp distribution. In the P3 rising beginning, posterior negative deflections in the LVF (Nd) and anterior positive deflections (Pd) in the UVF were observed. Under color cueing, P3 amplitude was reduced in the UVF accompanied by no behavioral effects. These results suggest that different patterns of brain activation can be obtained in upper and lower visual fields under spatial- and non-spatial cueing conditions.

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1. Introduction

When an uninformative peripheral cue appears in our visual field it automatically attracts our attention. If within a short time interval (approximately 250 ms following the cue) a target is presented at the same location as the cue, response times (RTs) are faster for that target than for a target appearing at a different location. However, if the time between the cue and the target is longer, RTs for targets at the cued location become slower. This effect was firstly explained as an inhibitory mechanism that prevents the processing of information appearing at explored locations to optimize the orienting of the visual system to novelty (Posner and Cohen, 1984), and it was later called Inhibition of Return (IOR; Posner et al., 1985). Since its discovery, IOR has been observed in a wide variety of experimental situations within the visual, auditory, and tactile modalities (e.g., Spence et al., 2000). IOR has also been observed across a variety of tasks, including detection, localization, and discrimination (see Klein (2000) for a review), and even in natural scenes (Klein and MacIness, 1999). IOR-like effects have also been

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observed to non-spatial dimensions of both cue and target stimuli such as color, shape, and semantics (non-spatial IOR; see, for example Chen et al., 2010; Fuentes et al., 1999; Hu et al., 2011). This ubiquity suggests that the mechanisms underlying IOR are important for the selection of information.

Nevertheless, the neural substrates and functional significance of IOR are still under debate. Current evidence indicates that IOR may arise from a combination of inhibited perceptual processing (Handy et al., 1999; McDonald et al., 1999; Prime and Ward, 2004; Prime et al., 2006), a more conservative response criterion on cued trials relative to uncued trials (Ivanoff and Klein, 2001, 2006), and an inhibition of motor (Pasttöter et al., 2008) and oculomotor programming (Ro et al., 2000). Given the evidence supporting several mechanisms, it has been proposed that IOR may arise from multiple processes (Kingstone and Pratt, 1999). In this context, Taylor and Klein (2000) proposed two mutually exclusive forms of IOR that depend essentially on whether the oculomotor system is activated (the motor form) or suppressed (the perceptual/attentional form). These forms have been recently observed both in behavioral execution and in visual event-related potential (ERP) results (Hilchey et al., 2013; Satel et al., 2013). Besides the probable implication of several processes in the generation of IOR, a reason for the current uncertainty on its origins may be related to

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several experimental factors affecting the presence, time course, and magnitude of IOR (Klein, 2000). In this regard, the most extensively used design to explore the effects of IOR has been the cue-target paradigm in the visual modality (for a review, see Klein, 2000). In this paradigm, a peripheral cue is presented before the target stimulus at different cue-to-target time intervals (cue-to-target stimulus onset asynchrony, CTOA), and the differences between the responses to cued and uncued targets are examined. The fact that to obtain an IOR effect a CTOA longer than approximately 250 ms is necessary has been attributed to the need to disengage attention from the cued location before the presentation of the target stimulus (Posner et al., 1985; but see, for example, Chica and Lupiáñez, 2009; Riggio et al., 2004). However, the cue-target paradigm does not assure that the attentional focus has been disengaged from the cue at the time of target presentation (Prime et al., 2006). To overcome this limitation, an alternative paradigm, called the 'cue-back design', presents a second cue (the cue-back) during the CTOA interval at central fixation. This cue-back does not share any characteristic with either the cue or the target and plays the only role of attracting attention away from the cue to ensure that it has been reoriented away from the cued location.

Another factor that may underlie the current uncertainty about the functional locus of the IOR effect is that related to the arrangement of the stimuli in the visual field. In this sense, the presentation of the stimuli along the horizontal axis has been one of the most frequently employed in this context (e.g. Fuchs and Ansorge, 2012; Taylor and Klein, 1998a; Wascher and Tipper, 2004). This arrangement, however, may result in an interaction of IOR effects with other related to the spatial relationships between the location of the target stimulus and the response hand (S-R compatibility). One of the most known is the Simon effect, which has been proposed to interact with IOR (see Ivanoff et al. (2002) for a review; Wang et al., 2013). To overcome possible interactions between IOR and spatial S–R compatibility effects, tasks presenting the stimuli along the vertical axis can be employed. Importantly, the perceptual characteristics of our visual hemifields along the vertical axis present several asymmetries (see Karim and Kojima (2010) for a recent review). On one hand, behavioral studies have found vertical asymmetries favoring the lower visual field (LVF) in contrast-sensitivity (Cameron et al., 2002; Carrasco et al., 2002), spatial resolution (Carrasco et al., 2002; Rezec and Dobkins, 2004), orientation (Raymond, 1994) and hue (Levine and McAnany, 2005). On the other hand, neurophysiological studies have also confirmed the higher sensitivity of the LVF to contrast patterns (Portin et al., 1999), high contrast checkerboards (Fioretto et al., 1995), and non-attended color (Czigler et al., 2004) or movement direction changes (Amenedo et al., 2007). Moreover, when studying visual ERP components, different patterns can be recorded due to the orientation of the cerebral tissue involved in the analysis of the stimuli, depending on the location in the visual field where stimuli are presented (Di Russo et al., 2001; Chica et al., 2010). Consequently, a main objective of the present research was to explore cueing effects with a vertical arrangement of stimuli, free of S-R compatibility effects.

The existing difficulty to characterize the IOR functional significance and its neural locus, led several research groups to examine the underlying electrophysiological mechanisms of behavioral IOR effects, from target presentation to response execution. These studies revealed that it could be possible that a neural effect associated with IOR happens without its concomitant behavioral expression, as Klein (2000) has argued. In this sense, P1 and N1 components, related to information processing in visual areas, and known to be modulated by attention (for a review, see Luck et al. (2000) and Satel et al. (2013)) have been the most studied in IOR research. In this context, previous studies have found amplitude reductions in the P1 component for spatially cued targets (Chica and Lupiáñez, 2009; Chica et al., 2010; McDonald et al., 1999; Prime and Jolicoeur, 2009; Prime and Ward, 2004, 2006; Satel et al., 2013; Tian and Yao, 2008; Tian et al., 2011b; van der Lubbe et al., 2005; Wascher and Tipper, 2004), even when slower reaction times (RTs) were not observed (Doallo et al., 2004; Eimer, 1994; Hopfinger and Mangun, 1998). These effects have been interpreted as reflecting a suppression or inhibition of perceptual processing in visual areas of previously cued stimuli. However, no effects of IOR on P1 have also been reported (Hopfinger and Mangun, 2001; McDonald et al., 1999; Prime and Ward, 2006; van der Lubbe et al., 2005). The N1 component, which is considered as an electrophysiological index of discrimination processes within the focus of visuospatial attention (Vogel and Luck, 2000), has showed more divergent effects of IOR. Thus, reduced N1 amplitude in cued trials has been mainly observed in those studies using designs that included a cue-back stimulus, and in studies requiring a discrimination task (Prime and Ward, 2004, 2006; Prime et al., 2006; Prime and Jolicoeur, 2009). In other designs, enhanced N1 amplitude was found both along with (McDonald et al., 1999; Tian and Yao, 2008) or without (Eimer, 1994) a behavioral IOR effect. Another ERP that has shown cueing effects is the P3 component. The IOR effect on RTs has been also found to be associated with enhanced P3 amplitude on cued trials (McDonald et al., 1999). However, this effect has not been always reported, since Hopfinger and Mangun (2001) and Zhang et al. (2012) did not find P3 modulations when behaviorally significant IOR effects were present. The effects of cueing on P3 have been interpreted as a post perceptual effect more related to endogenous attention processes than to pure IOR (Chica and Lupiáñez, 2009). The comparison of the ERP waveforms between cueing conditions led several groups to analyze negative differences within different latency ranges (called in general Negative difference, Nd) in the IOR context, although no consensus has been reached on their direct relation to IOR effects. Thus, McDonald et al. (1999) explained the Nd component observed in their study (increased negativity within 100–200 ms in cued trials) as an index of sensory refractoriness caused by response to the cue. Posteriorly, Wascher and Tipper (2004) described three independent Nd components: Nd150 (140-160 ms), Nd250 (240-260 ms) and Nd310 (300–320 ms). They related the Nd150 to sensory refractoriness in the cued location, the Nd250 to inhibitory processes associated with the demands of the task, and the latter, Nd310, observed only when a behaviorally IOR effect was found, to the effort to allocate the focus of attention to a previously inhibited location. However, Prime and Ward (2006) and Prime and Jolicoeur (2009) did not relate directly the processes underlying the Nd with the IOR generation per se. More recently, three differential waves (called Pd200, Nd240, and Nd280) have also been described associated to IOR effects (Tian et al., 2011a).

Taking all the above into account, the purpose of the present study was to explore the neurocognitive correlates (behavioral and ERP data) of spatial and non-spatial cueing effects. To overcome S–R compatibility effects that might interact with IOR effects, a cue-back task with stimuli in the vertical meridian was employed. Finally, due to the well-known vertical asymmetries in visual processing, we tested the possible differences between UVF and LVF when the location and color of target stimuli were cued in a color discrimination task.

2. Method

2.1. Participants

Twenty healthy naive volunteers (12 females) participated in the experiment. Participants mean age was 24.56 ± 5.86 (19–37 years), and two of them were left-handed. All participants reported having normal or corrected-to-normal vision. They obtained a monetary compensation for their participation.

2.2. Stimuli and experimental procedure

During the task (see Fig. 1), one central and two peripheral (external edge 4.5° of visual angle from the center of the screen) light gray boxes (RGB 200,200,200, $1.5^{\circ} \times 1.5^{\circ}$ of visual angle) were always present on the vertical meridian of a computer screen (100 Hz resolution). A

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