SPATIAL INHIBITION OF RETURN PROMOTES CHANGES IN RESPONSE-RELATED MU AND BETA OSCILLATORY PATTERNS

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Abstract—The possible role that response processes play in Inhibition of Return (IOR), traditionally associated with reduced or inhibited attentional processing of spatially cued target stimuli presented at cue-target intervals longer than 300 ms, is still under debate. Previous psychophysiological studies on response-related Electroencephalographic (EEG) activity and IOR have found divergent results. Considering that the ability to optimize our behavior not only resides in our capacity to inhibit the focus of attention from irrelevant information but also to inhibit or reduce motor activation associated with responses to that information, it is conceivable that response processes are also affected by IOR. In the present study, time-frequency (T-F) analyses were performed on EEG oscillatory activity between 2 and 40 Hz to check whether spatial IOR affects response preparation and execution during a visuospatial attention task. To avoid possible spatial stimulus-response compatibility effects and their interaction with the IOR effects, the stimuli were presented along the vertical meridian of the visual field. The results differed between lower and upper visual fields. In the lower visual field spatial IOR was related to a synchronization in the pre-movement mu band at bilateral precentral and central electrodes, and in the post-movement beta band at contralateral precentral and central electrodes, which may be associated with an attention-driven reduction of somatomotor processing prior to the execution of responses to relevant stimuli presented at previously cued locations followed by a post-movement deactivation of motor areas. In the upper visual field, spatial IOR was associated with a decrease in desynchronization around response execution in the beta band at contralateral postcentral electrodes that might indicate a late (last moment) reduction of motor activation when responding to spatially cued targets. The present results suggest that different response processes are affected by spatial IOR depending on the visual field

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INTRODUCTION

The limited capacity of human brain makes it impossible to incorporate all available information. Visuospatial attention studies have shown that attention-shifting processes provide adaptive benefits by allowing the brain to select the information relevant in each moment as a basis for other processes, such as memory, learning and decision-making, which are essential for adaptation and correct functioning in everyday life. In this context, Posner and Cohen (1984) found that when responding to targets previously signaled by a peripheral cue two possible effects are observed on reaction time (RT) depending on the time interval between the cue and the target presentation. When that time is shorter than 250-300 ms. RTs are faster (facilitation effect). At longer time intervals, however, RTs are slower. The authors explained this increase in RT as a mechanism that helps in selecting relevant information units by inhibiting attention from focusing on previously explored locations when there is enough time to process them. Posner et al. (1985) retrospectively named this mechanism Inhibition of Return (IOR).

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 tasks, and even in natural scenes (see Klein, 2000, for a review). However, at present no consensus has yet been reached regarding either the mechanisms of IOR or their functional significance.

The existing difficulty in characterizing the functional significance of IOR and its neural locus, led several research groups to examine the underlying electrophysiological mechanisms of behavioral IOR effects by means of event-related potential (ERP) analyses. Specifically, these ERP studies have mainly focused on stimulus-related components, and have shown that spatial IOR is frequently, but not always, associated with amplitude modulations in P1 and N1

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Abbreviations: ANOVA, analysis of variance: CTOA, cue-target onset asynchrony; EEG, Electroencephalographic; ERD, event-related desynchronization; ERP, event-related potential; ERS, event-related synchronization; ERSP, Event-Related Spectral Perturbation; fdr, false discovery rate; ICA, independent component analysis; IOR, Inhibition LRP, potential; of Return: lateralized readiness MEG. response-locked LRP: magnetoencephalography; R-LRP, RT reaction time; T–F, time–frequency; T-LRP, target-locked LRP.

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target-locked visual components. Such modulations have been generally interpreted as neural correlates of the effects of IOR on the perceptual–attentional processing of spatially cued target stimuli. Moreover, IOR effects on target-locked ERPs have resulted in other amplitude modulations in the ERP waveforms within latency intervals that do not coincide specifically with the peak of any component, and consisting in amplitude shifts whose functional interpretation is still under debate (see Gutiérrez-Domínguez et al., 2014).

However, the above-described IOR effects on targetlocked ERPs have not always been associated with behavioral IOR effects (i.e. slower RTs to cued targets; see for example Hopfinger and Mangun, 1998: McDonald et al., 1999; Doallo et al., 2004), suggesting that, possibly, response processing is also influenced by it (Kingstone and Pratt, 1999; Pastötter et al., 2008). Response-level explanations of IOR have received support from behavioral evidence showing that it might be associated with a more conservative response criterion on cued trials (Ivanoff and Klein, 2001), and that IOR can affect oculomotor programing (Ro et al., 2000). To explore more directly the response-related processes affected by IOR, Prime and Ward (2004, 2006) measured the effects of IOR on the lateralized readiness potential (LRP), and examined the possibility that responserelated effects of IOR may arise at either decisional or motor stages of response processing. To that end, they examined the target-locked LRP (T-LRP) and the response-locked LRP (R-LRP) components starting from the premise that if IOR arises from inhibition of motor processes, then the interval between the onset of the R-LRP and the response should be longer under IOR, while if IOR arises from decisional but not motor processes, then only the interval between the target presentation and the response would be affected by IOR (affecting the latency of the T-LRP). They found IOR effects on T-LRP latency but not on R-LRP latency, concluding that IOR may not be related to response preparation timing but only to pre-motor selection processes. More recently, Amenedo et al. (2014) examined the amplitude changes in R-LRP, and found that IOR was related to a significant amplitude reduction of this component when responding to previously cued targets, suggesting that response preparation could be affected when responding to targets presented at previously cued locations.

Event-related changes in Electroencephalographic (EEG) activity may be studied with different approaches. One of the most frequently employed has been the ERP technique, which is based on the measurement of amplitude changes in the ongoing EEG activity time-locked to stimulus presentation or to response execution. An alternative and complementary approach is the measurement of event-related changes in frequency oscillations that occur in the ongoing EEG activity in association with stimulus presentation or response production. One of the most extended methods for the analysis of EEG oscillations is the so-called time–frequency (T–F) analysis that allows examination of the spatio-temporal changes in spectral power within different frequencies relative to a baseline

period and related to stimulus or response processing (see Roach and Mathalon, 2008 for a comprehensive review on ERP and T–F methodologies).

In the context of movement execution, EEG activity within sensorimotor areas of the human brain has long been known to exhibit oscillatory behavior, which makes the T-F approach suitable for studying possible effects of IOR on response processes. Of particular interest have been oscillations within two specific frequency bands, the mu (8-14 Hz) and beta (15-30 Hz) bands, as they have been shown to be modulated during and following the preparation and performance of voluntary movements (Salmelin et al., 1995; Pfurtscheller et al., 1996a,b; Leocani et al., 1997; Cassim et al., 2001; Jurkiewicz et al., 2006; Parkes et al., 2006), passive movements (Cassim et al., 2001), imagined movement (Pfurtscheller et al., 2005, 2006), and even tactile stimulation (Neuper and Pfurtscheller, 2001; Cheyne et al., 2003; Gaetz and Cheyne, 2006). Modulation of the mu and beta band oscillations that accompany voluntary movements has been described and takes one of two forms. Beginning as early as 2 s prior to movement initiation (Pfurtscheller and Berghold, 1989; Leocani et al., 1997), a reduction in power in both the mu and beta frequency bands, known as event-related desynchronization (ERD), has been observed over sensorimotor areas with a contralateral predominance in the case of the beta band (see Pfurtscheller and Lopes da Silva, 1999 for review) and more bilateral for the mu band (Salmelin et al., 1995) although contralateral predominance has also been shown in this frequency band (see Pfurtscheller et al., 1996a, for review). Desynchronization of these oscillations, the result of asynchronous activity within these cortical networks, has been related to neural activation (Pfurtscheller and Berghold, 1989). Following movement termination, while mu power returns slowly to baseline (Salmelin and Hari, 1994; Salmelin et al., 1995; Leocani et al., 1997), beta power consistently returns to and exceeds premovement levels (Pfurtscheller et al., 1996a; Jurkiewicz et al., 2006). This event, known as event-related synchronization (ERS) begins within several hundred milliseconds of movement termination and persists for several hundred more. Although it is generally believed that ERS reflects a neural deactivation, the socalled 'idling' hypothesis (Pfurtscheller et al., 1996a; Cassim et al., 2001), this specific beta band ERS that follows movement termination is known as postmovement beta rebound (PMBR) and has been suggested to represent an inhibition of motor cortex (Salmelin et al., 1995; Jurkiewicz et al., 2006) or a sensorimotor reafference (Cassim et al., 2001) after movement execution.

Exploring spatial IOR effects on response-related EEG oscillatory activity by means of T–F analyses, Pastötter et al. (2008) examined changes in ERS–ERD patterns (temporal spectral evolution analysis, Hari and Salmelin, 1997) restricted to the pre-movement 15–25 Hz beta band in two IOR designs: a target–target design, and a cue-target design. They found that in the target–target design behavioral IOR was associated with an increase in contralateral beta ERS while in the cue-target design IOR was related to a decrease in beta

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