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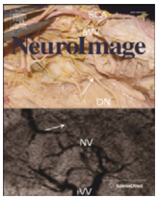

Gearing up for action: Attentive tracking dynamically tunes sensory and motor oscillations in the *alpha* and *beta* band[☆]

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ABSTRACT

Allocation of attention during goal-directed behavior entails simultaneous processing of relevant and attenuation of irrelevant information. How the brain delegates such processes when confronted with dynamic (biological motion) stimuli and harnesses relevant sensory information for sculpting prospective responses remains unclear. We analyzed neuromagnetic signals that were recorded while participants attentively tracked an actor's pointing movement that ended at the location where subsequently the response-cue indicated the required response. We found the observers' spatial allocation of attention to be dynamically reflected in lateralized parieto-occipital *alpha* (8–12 Hz) activity and to have a lasting influence on motor preparation. Specifically, *beta* (16–25 Hz) power modulation reflected observers' tendency to selectively prepare for a spatially compatible response even before knowing the required one. We discuss the observed frequency-specific and temporally evolving neural activity within a framework of integrated visuomotor processing and point towards possible implications about the mechanisms involved in action observation.

Introduction

When interacting with our environment, we face the problem of selecting among a host of action possibilities (Cisek and Kalaska, 2010) that are afforded by different agents and/or objects that attract our attention to varying degrees (e.g., Gibson, 1966; Grèzes et al., 2003). An effective way to resolve this challenge is through directed visuo-spatial attention, which has been repeatedly shown to improve processing of information falling within the locus of attention while reducing the interference from competing sensory information occurring elsewhere within the visual field (Desimone, 1998; Desimone and Duncan, 1995; Posner et al., 1980). Attention studies have frequently examined static stimulation conditions, however, and in part constrained by neuroimaging methods with limited temporal resolution (Culham et al., 1998), much less is known about the brain mechanisms supporting dynamic attention processes (e.g., as involved in attentional tracking of moving objects in space). This is particularly so in everyday contexts such as action observation, an activity known to engage both attention (Belopolsky et al., 2008) and motor systems (Koelewijn et al., 2008).

Insights into the role of brain oscillations involved in spatial attention processes have particularly been gained through human neurophysiological studies employing the endogenous pre-cuing paradigm (Posner et al., 1980). In this paradigm, a cue informs about the likely location of a laterally presented target stimulus. After a delay period (cue–target interval of ~1.0 to 2.5 s) the target stimulus then demands participants to make a perceptual detection (Thut et al., 2006) or discrimination response (Siegel et al., 2008). Cumulative research evidence has shown that lateralized parieto-occipital *alpha* (8–12 Hz) oscillations are strongly associated with the deployment of spatial attention (Capila et al., 2012; Thut et al., 2006) as well as modulated by spatial certainty (Gould et al., 2011). Specifically, the decrease of *alpha* oscillation amplitude in the hemisphere contralateral to the attended visual hemifield has been related to enhanced processing of information at the attended location, whereas the increase (or constant) *alpha* oscillation amplitude in the hemisphere ipsilateral to the attended visual hemifield has been related to the suppression of processing of information at the unattended location (Rihs et al., 2009).

In addition to the observation that *alpha* neural activity is associated with the functional inhibition of task-irrelevant brain areas (Händel et al., 2010; Jensen and Mazaheri, 2010; Kelly et al., 2006), other studies have also demonstrated that lateralized *alpha* amplitude is (inversely) related to perceptual performance (Hanslmayr et al., 2007; van Dijk et al., 2008; Wyart and Tallon-Baudry, 2009). Thus, improvement of both perceptual and motor performance correlates with the suppression of parieto-occipital *alpha* oscillations (Foxe and Snyder, 2011). Since occipital *alpha* oscillations have been linked to excitability changes of

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visual areas (Romei et al., 2008a, 2008b, 2010) modulations of perceptual performance are not surprising. However, response times depend on the activation state of motor areas that is typically reflected in *beta* (16–35 Hz) oscillations (Engel and Fries, 2010). In fact, *beta* oscillations in cortical motor areas are known to have a causal effect on movement duration, force-generation, and inhibition (Joundi et al., 2012; Pogosyan et al., 2009) and are modulated during action observation (Kilner et al., 2009; Press et al., 2011). Yet, the specific contributions of parieto-occipital *alpha* and motor *beta* oscillations to perceptually (e.g., spatially) invigorated action preparation remain unclear. Indeed, we know relatively little about how *alpha* oscillations (i) mediate the expectancy-related attention process, and (ii) influence the on-going neural dynamics involved in shaping our prospective actions when spatial "cue" information is dynamically provided rather than statically some time before target onset. However, the former scenario mimics an everyday situation (e.g., driving through a busy crossroad where the movement of other vehicles and pedestrians require simultaneous monitoring) wherein we are required to pay attention (overtly or covertly) to dynamically moving object(s) of interest before deciding which action will be taken shortly.

The present study investigates how attention is allocated in the presence of dynamic biological motion stimuli (i.e., the arm movement of an actor) and how on-going anticipatory motor activation is influenced. More specifically, we used magnetoencephalography (MEG) to monitor participants' *alpha* and *beta* oscillations while they observed an actor making pointing movements towards a lateral target (Fig. 1). At the end of the pointing movement the color of the target changed and cued the participant to perform a right or left hand response. Importantly, the actor's pointing movements were either targeted towards an endpoint in the same hemifield (straight movement) or one located in the opposite hemifield (crossed movement), thereby validly indicating the position of the response cue but not that of the to-be-executed response. The task as a whole requires participants i) to detect/discriminate the pointing hand in the spatial periphery, ii) to attentively track the changing spatial location of the pointing hand, and iii) to discriminate the response cue after the pointing movement reached its endpoint location. This modified 'Simon-task' (Simon, 1969) provides a useful experimental paradigm for a number of reasons. First, it fulfills the attention processing criteria as employed in previous visuo-spatial attention research. Second, it grounds the task within an ecological framework as we deal with both static and dynamic stimuli in our daily interactions with others. Third, and importantly, our modified task version allows us to temporally segregate actual motor from sensory processing and to focus specifically on the attention-related processes prior to any actual movement onset. Furthermore, presenting straight and crossed arm movements allows us to test whether covert motor activation induced during action observation (Koelewijn et al., 2008) relates to the moving limb of the actor (effector mirroring) or rather to the spatial position of the arm (position mirroring). Whereas behavioral evidence regarding this issue is mixed (Belopolsky et al., 2008; Bertenthal et al., 2006), to our knowledge, there is only one functional neuroimaging (MEG) study that addressed this issue (Kilner et al., 2009), finding evidence against the effector mirroring view.

Our study specifically focuses on the sensory and cognitive processes leading up to motor response anticipation. We hypothesize that the active allocation of attention to incoming visuo-spatial information serves to dynamically update predictions about the behaviorally relevant movement endpoint (which could be located either in observers' left or right visual hemifield). Consequently, the emerging *alpha* lateralization in parieto-occipital brain regions should sensitively index the associated shift in spatial attention. It is also known that *beta* oscillations in cortical motor regions are related to the temporal prediction of sensorimotor events (Fujioka et al., 2012; Saleh et al., 2010) and the state of motor preparation as a function of response certainty (Tzagarakis et al., 2010). Therefore, we further hypothesize to observe dynamic changes in *beta* lateralization reflecting anticipatory processes, e.g., response bias, and/or influences of sensorimotor information that can be expected to change during the attentive observation of the actor's pointing

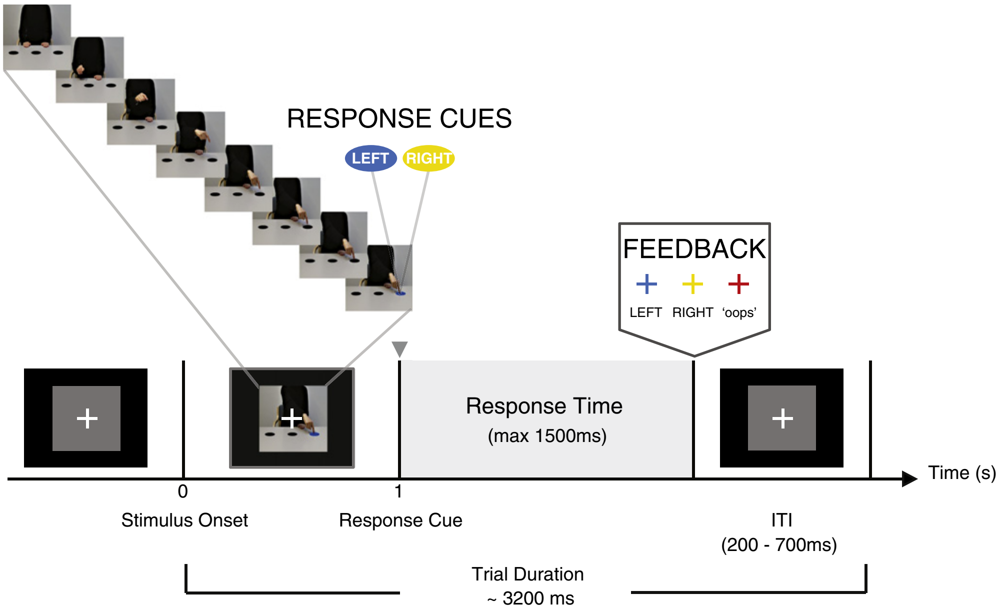

Fig. 1. The sequence of events in an experimental trial. A gray background screen of equal size as the movie frames (13° × 13° visual angle) was presented for a randomized inter-trial interval (ITI) of 200 to 700 ms. The movie (60 fps) started with the presentation of the first frame at $t = 0$ ms. The last movie frame and the response cue appeared at $t = 1000$ ms, and remained on screen showing the actor with the pointing hand in its end position and the other hand in a resting position. A target color change from black to blue (yellow) necessitated a left (right) index response within 1500 ms post response cue onset. In trials requiring no response, the randomized ITI followed 1500 ms after the end of the pointing movement. Throughout the experimental session a white fixation cross was centered in the middle of the stimuli, and it was also present during the randomized inter-trial intervals when the movie still-frames were reset to a gray background. Participants were provided with response feedback during the ITI in the form of a color change in the fixation cross that corresponded to their actual response (i.e. blue for 'left', yellow for 'right', and red for a 'wrong' response, such as an incorrect or delayed response).