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The peak frequency of motor-related gamma oscillations is modulated by response competition

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ABSTRACT

Movement execution generally occurs in an environment with numerous distractors, and requires the selection of a motor plan from multiple possible alternatives. However, the impact of such distractors on cortical motor function during movement remains largely unknown. Previous studies have identified two movement-related oscillatory responses that are critical to motor planning and execution, and these responses include the perimovement beta event-related desynchronization (ERD) and the movement-related gamma synchronization (MRGS). In the current study, we investigate how visual distractors cuing alternative movements modulate the beta ERD and MRGS responses. To this end, we recorded magnetoencephalography (MEG) during an arrow-based version of the Eriksen flanker task in 42 healthy adults. All MEG data were transformed in to the time-frequency domain and the beta ERD and MRGS responses were imaged using a beamformer. Virtual sensors (voxel time series) were then extracted from the peak voxels of each response for the congruent and incongruent flanker conditions separately, and these data were examined for conditional differences during the movement. Our results indicated that participants exhibited the classic "flanker effect," as they responded significantly slower during incongruent relative to congruent trials. Our most important MEG finding was a significant increase in the peak frequency of the MRGS in the incongruent compared to the congruent condition, with no conditional effect on response amplitude. In addition, we found significantly stronger peri-movement beta ERD responses in the ipsilateral motor cortex during incongruent compared to congruent trials, but no conditional effect on frequency. These data are the first to show that the peak frequency of the MRGS response is linked to the task parameters, and varies from trial to trial in individual participants. More globally, these data suggest that beta and gamma oscillations are modulated by visual distractors causing response competition.

Introduction

In daily life, movement selection is rarely a straightforward process. Multiple movement options are almost always available, and competing environmental cues and distractions are ubiquitously present. One classic experiment that captures this phenomenon is the Eriksen flanker task (Eriksen and Eriksen, 1974). Briefly, during the Eriksen flanker task, participants attend to a central stimulus that is "flanked" by non-target stimuli. In the "congruent" or non-distractor condition, the flanking stimuli indicate the same response as the target stimulus. However, in the "incongruent" or distractor condition, the flanking stimuli indicate a conflicting, often opposite response to the target stimulus. The classic finding in this task is an increase in reaction time in the incongruent relative to the congruent condition. Many studies have identified the brain regions serving congruent and incongruent stimuli processing in the context of selective attention and/or conflict monitoring (e.g., Botvinick et al., 1999; Bunge et al., 2002; Cavanagh et al., 2009; Clayson and Larson, 2011; Cohen and van Gaal, 2014; Danielmeier et al., 2009; Hazeltine et al., 2000; Hochman et al., 2014; Larson et al., 2012; Nigbur et al., 2011, 2012; Padrao et al., 2015; Tillman and Wiens, 2011; others). However, very few studies have focused on the motor response aspect of the task, which is unfortunate as it could provide critical insights on how distracting stimuli and response conflict modulate movement selection during ongoing cognitive processing.

Recent neurophysiological studies of motor control in humans have largely focused on two movement-related oscillatory responses. First, prior to and during movement, there is an event-related desynchronization (ERD) in the beta band (\sim 14–30 Hz), termed the peri-movement

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beta ERD (Cheyne et al., 2006; Engel and Fries, 2010; Gaetz et al., 2010; Heinrichs-Graham and Wilson, 2015, 2016; Heinrichs-Graham et al., 2014; Jurkiewicz et al., 2006; Pfurtscheller and Lopes da Silva, 1999; Wilson et al., 2010, 2011, 2014). This response typically persists from about 1.0 s prior to movement onset until about 0.5 s after movement and peaks in the bilateral precentral gyri, with stronger responses found contralateral to movement. Other regions that generate a peri-movement beta ERD, especially during complex movements, include the supplementary motor area (SMA), premotor cortices, parietal cortices, and cerebellum (Cheyne et al., 2006; Heinrichs-Graham et al., 2016; Heinrichs-Graham and Wilson, 2015; Kurz et al., 2014; Wilson et al., 2010, 2011, 2014). Multiple studies have recently probed the functional roles of the peri-movement beta ERD, and this work overwhelmingly supports the notion that this response is crucial to motor planning and movement selection. For example, the amplitude of the beta ERD is known to be significantly modulated by complexity of the movement to be executed (Heinrichs-Graham and Wilson, 2015), the certainty of the pending movement direction (Doyle et al., 2005; Kaiser et al., 2001; Tzagarakis et al., 2010), the similarity between potential movement plans (Grent-'t-Jong et al., 2014; Praamstra et al., 2009), and other cue-related factors (Alegre et al., 2003; Heinrichs-Graham et al., 2016). Of note, there is a resynchronization in the beta band that follows movement termination, termed the post-movement beta rebound (PMBR), but given the time course of this response, it is not thought to be directly involved in motor planning or execution (Alegre et al., 2004, 2008; Fry et al., 2016; Heinrichs-Graham et al., 2017; Houdayer et al., 2006; Jurkiewicz et al., 2006; Parkes et al., 2006; Pfurtscheller and Lopes da Silva, 1999; Reyns et al., 2008; Solis-Escalante et al., 2012; Wilson et al., 2010).

In addition to the beta responses, there is also increased gamma activity during movement called the movement-related gamma synchronization (MRGS). The MRGS occurs in the 60-90 Hz range and typically starts about 0.05 s prior to the movement and extends until about 0.1 s after movement onset. This response is primarily isolated to the precentral gyrus contralateral to movement, though it has also been found in the SMA (Cheyne et al., 2008; Gaetz et al., 2010, 2011; Muthukumaraswamy, 2010; Wilson et al., 2010). Very few studies have focused on the functional role of the MRGS, but given the temporal characteristics of the response, and its relative isolation in the primary motor cortex, the MRGS has long been thought to be the oscillatory signature of the motor execution signal. For example, Muthukumaraswamy (2010) used magnetoencephalography (MEG) and several simple motor tasks to identify the basic parameter space of the MRGS response. He found bursts of MRGS activity at the onset of both simple transient movements and isometric forces, and that this burst did not persist for the duration of the isometric force. However, during repetitive transient movements, there was a MRGS at the onset of each movement. These data suggest that the MRGS functions specifically as a movement onset response, as it is not sustained throughout motor execution.

While these motor-related oscillations have been widely studied, the potential impact of interference and response conflict in modulating these neural responses remains largely unknown. One recent study used a modified Eriksen flanker task and MEG to investigate how these parameters (congruent vs. incongruent) altered the peri-movement beta ERD and MRGS (Grent-'t-Jong et al., 2013). They found that both left sensorimotor beta ERD (contralateral to movement) and mid-frontal MRGS began significantly earlier during incongruent compared to congruent trials, which resulted in a significantly larger beta ERD and MRGS during very early components of each response. However, since these findings were only observed with respect to movement onset (and not stimulus onset), one interpretation of these data is that the findings largely reflect the differential amount of time between stimulus onset and the motor response in congruent relative to incongruent trials. In other words, when the motor response is defined as time zero, the stimulus occurred longer ago in the incongruent relative to the congruent condition, and this alone could underlie such oscillatory

differences early in the time course. This scenario seems especially plausible, as one of the main findings was that the conditional difference in the mid-frontal MRGS was significantly correlated with a stronger flanker effect (i.e., larger reaction time differences between congruent and incongruent trials; Grent-'t-Jong et al., 2013). Another MEG study also probed the impact of interference on motor oscillations, but instead of the flanker task they utilized a conceptually similar multi-source response interference task (Gaetz et al., 2013). As with the flanker task, a key finding was that the MRGS in the primary motor cortex contralateral to movement began earlier during interference trials compared to trials without response interference (Gaetz et al., 2013). Again, these results could reflect differences in reaction time, as participants responded slower in the interference trials and thus stimulus onset occurred longer ago relative to trials without interference. In sum, neither of these studies found differences in motor-related oscillations during the movement (when the responses peak), which raises the question of whether the findings reflect specific motor control differences or just prolonged processing in the interference/response conflict conditions.

The goal of the current study was to clarify the role of motor-related oscillatory activity in the sensorimotor cortices in the context of visual interference causing response competition. To this end, healthy adult participants performed a unimanual, arrow-based version of the Erickson flanker task during MEG. The resulting data were imaged in the timefrequency domain and virtual sensors (voxel time series) were extracted to evaluate the temporal dynamics of both the beta ERD and the MRGS. We hypothesized that the beta ERD and MRGS would be uniquely altered during the actual response (i.e., movement) during the incongruent relative to congruent trials, indicative of each response's unique role in movement selection and execution.

Methods

Participants

Forty-seven healthy adults (22 females) completed the study. Five participants (3 females) were excluded from analysis due to poor performance, MEG artifacts, and/or no significant movement-related oscillatory response. The mean age of the remaining 42 participants was 27.17 years (SD: 4.53, range: 20–44 years). A total of 7 participants in the final sample were left-handed. Exclusionary criteria included any medical diagnosis affecting CNS function (e.g., psychiatric and/or neurological disease), known brain neoplasm or lesion, history of significant head trauma, current substance dependence, and ferromagnetic implants. Written informed consent was obtained from each participant following the guidelines of the University of Nebraska Medical Center's Institutional Review Board, who approved the study protocol.

Stimuli and task

Participants performed an arrow-based version of the Eriksen flanker task (Eriksen and Eriksen, 1974) while seated in a nonmagnetic chair within the magnetically-shielded room. Each trial began with a fixation that was presented for an interval of 1.5 ± 0.05 s. A row of 5 arrows was then presented for 2.5 s, and participants were instructed to respond with their right hand as to the direction of the middle arrow by pressing their index finger (left arrow) or middle finger (right arrow). In congruent trials, the middle arrow was pointing the same direction as the flanker arrows, while in the incongruent trials, the middle arrow was pointing in the opposite direction of the flanker arrows (Fig. 1). Trials were pseudo-randomized and equally split between congruent and incongruent conditions, with left and right pointing arrows being equally represented in each condition. A total of 200 trials were presented, making the overall MEG recording time about 14 min for the task.

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