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Theta-band EEG Activity over Sensorimotor Regions is Modulated by Expected Visual Reafferent Feedback During Reach Planning

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Abstract—Activity in the primary motor cortex (M1) during reach planning is known to be correlated with the upcoming kinetics and kinematics of the hand. Yet recent work using visual-motor dissociation tasks suggests that M1 activity is also correlated with the visual consequences of an action, independent of the actual hand displacement. The goal of the present work was to investigate whether oscillatory activity over sensorimotor regions is modulated by the expectancy of visual reafferent feedback during reach planning. While recording electroencephalography (EEG), participants executed hand-reaching movements in a single direction (i.e., straight-ahead of midline) throughout the entire experiment. Visual feedback of the hand was provided with a cursor and was manipulated. Specifically, before each trial, participants were precued as to the nature of the upcoming visual feedback, which could be spatially congruent with the hand, rotated leftward or rightward by 20° or not provided at all. Results revealed that planning-related EEG activity at contralateral central electrodes was strongly modulated in the theta-band (3–7 Hz) depending on whether visual feedback would be available or not. In contrast, contralateral beta-band (15–30 Hz) activity did not differ across conditions. These results demonstrate that low-frequency oscillatory dynamics during reach planning depend upon the upcoming availability of visual feedback. This may relate to predicting the visual consequences of the movement or to setting different feedback gains necessary for visually guided vs. non-visually guided movements.

Key words: EEG oscillations, visuospatial attention, sensory predictions.

INTRODUCTION

An important issue in motor control relates to the processes at play during the planning of goal-directed reaching movements. It has long been known that activity within the primary motor cortex (M1) is tightly coupled to the physical displacement of the hand. Indeed, considerable electrophysiological studies in monkeys (Evarts, 1968; Georgopoulos et al., 1982; Scott and Kalaska, 1997; Sergio and Kalaska, 1997, 2002; Kakei et al., 1999; Moran and Schwartz, 1999; Mehring et al., 2003; Kilavik et al., 2012) and neuroimaging studies in humans (Eisenberg et al., 2010; Barany et al., 2014; Fabbri et al., 2014) have provided evidence that activity in M1 correlates with the kinetics and kinematics of upcoming reaching movements.

Yet, movement planning not only requires the brain to specify the upcoming displacement of the hand, but also to predict its associated sensory consequences (Wolpert and Flanagan, 2001). Interestingly, there is increasing support for the notion that M1 also contributes to sensory predictions. In fact, a key postulate of predictive coding theory, which is based on the principle of active inference, is that the output of M1 is not motor commands per se, but rather predictions of the sensory consequences of action (Friston et al., 2009; Adams et al., 2013; Gandolla et al., 2014). In support, behavioral phenomena that depend upon accurate somatosensory predictions, such as tactile suppression and anticipatory grip force modulation, have been shown to be influenced by M1 stimulation, suggesting a role of M1 in these predictions (Chouinard et al., 2005; Nowak et al., 2005; Voss et al., 2007). Recently, Eisenberg et al. (2011) provided evidence that preparatory activity in M1 also encodes the visual consequences of the movement. They used visuomotor rotation to dissociate the direction of visual feedback from that of the hand while probing M1 activity with functional magnetic resonance imaging. Interestingly, they observed significant positive correlations between patterns of blood oxygen-level-dependent (BOLD) responses for trials that were matched in terms

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Abbreviations: BOLD, blood oxygen-level-dependent; CSD, current source density; EEG, electroencephalography; ERSPs, event-related spectral perturbations; FDR, false discovery rate; ICs, independent components; LRP, lateralized readiness potential; M1, primary motor cortex; MT, movement time; ROIs, regions of interest; RT, reaction time.

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of upcoming visual feedback direction, irrespective of hand direction. This demonstrates that reach planning activity in M1 is sensitive to visual aspects of the movement, reflecting either the expected visual feedback of the hand and/or the visual goal [see also Krasovsky et al. (2014)].

The objective of the present study was to assess whether planning-related electroencephalographic (EEG) activity over sensorimotor regions is modulated by the expectancy of visual reafferent feedback of the hand. It is well established that reach planning incurs modulations across a broad spectrum of oscillatory frequencies, including the theta- (3–7 Hz), alpha- (or mu) (8–14 Hz) and beta-bands (15–30 Hz) (Pfurtscheller and Lopes da Silva, 1999; Pfurtscheller et al., 2003; Gilbertson et al., 2005; Pineda, 2005; Perfetti et al., 2011; Kilavik et al., 2013). Yet it is still unclear whether these modulations depend mainly upon the kinetics and kinematics of an upcoming movement, or whether they also depend upon the visual consequences of the movement (see Kilavik et al., 2014). Recently, Hughes and Waszak (2011) investigated the lateralized readiness potential (LRP), which is thought to be generated within M1 (Coles, 1989; Leuthold and Jentzsch, 2002; Leuthold et al., 2004), in a task in which a keypress could either trigger the onset of a visual checkerboard or not. They found an increase in the LRP when a movement was associated with the appearance of the visual stimulus as compared to when it was not, and interpreted this as a cortical correlate of the predicted action effect. Given that LRPs are reflected mainly in low-frequency activity (~3 Hz; Waldert et al., 2008), this finding is consistent with recent evidence suggesting that low-frequency oscillations, notably in the theta-band, play a role in the predictive anticipation of sensory events by controlling neuronal excitability (Saleh et al., 2010; Schroeder et al., 2010; Arnal et al., 2011; Cravo et al., 2011; Arnal and Giraud, 2012; Tomassini et al., 2017). In this light, manipulating the nature of the visual feedback associated with an upcoming movement may influence low-frequency EEG activity over sensorimotor regions during reach planning.

To test this hypothesis, a reaching task was designed in which participants were instructed to move their hand toward a single target location throughout the entire experiment. At the beginning of each trial, they were precued as to the nature of the upcoming hand visual feedback, which could be either veridical, rotated leftward or rightward by 20°, or not provided at all. This allowed us to compare reach planning for movements with similar physical hand displacements (and thus similar motor commands), but for which only the expected visual reafferent feedback differed. While the main focus of the present work was on sensorimotor regions, alpha-band activity over parieto-occipital regions was also investigated. These regions are well known to be implicated in visuospatial attention, with alpha oscillations allowing to regulate their excitability and ensuing processing of task-relevant visual information (Rihs et al., 2009; Van Der Werf et al., 2010; Bauer et al., 2012; Marshall et al., 2015). Hence a secondary objective of this work was to assess possible alpha-band modulations depending on the direction of expected visual feedback.

EXPERIMENTAL PROCEDURES

Participants

Fifteen healthy right-handed participants (5 women), between 17 and 38 years old (mean age 23.1 ± 4.8 years old) took part in the experiment. They had normal or corrected to normal vision, and reported no history of neurological or psychiatric illnesses. They provided an informed consent which was validated by the ethics committee of the Centre Hospitalier de l'Université de Sherbrooke. Given the absence of prior studies addressing the current issue (manipulation of expected feedback but similar kinematics), a proper power analysis could not be performed. Instead, sample size was based upon EEG studies investigating event-related potentials or oscillatory activity using reaching tasks most closely related to the present one (Naranjo et al., 2007; $n = 9$; Praamstra et al., 2009; $n = 14$ and $n = 13$ in separate experiments; Perfetti et al., 2011; $n = 13$; Rawle et al., 2012; $n = 20$).

Apparatus

The experimental setup consisted of a table supporting a computer monitor which projected visual stimuli on a semi-reflective mirror, preventing participants from seeing their hand. The monitor (20-inch Dell P1130; resolution: 1024 × 768; refresh rate: 150 Hz) was mounted face down 29 cm above the horizontal mirror. The mirror itself was mounted 29 cm above the table. With this setup the target appeared to be projected directly onto the surface of the table on the same plane as the hand. The starting base consisted of an L-shaped piece of aluminum fixed to the table. It was located 15 cm in front of participants' chest along the midline, and was defined as coordinates (0, 0). A two-joint planar manipulandum was placed on the table and was held by participants via a stylus located at its mobile end. The manipulandum was custom-built with two lightweight metal rods (48 and 45 cm respectively), with the fixed end attached to the upper left of the table. A thin sheet of smooth plastic was put on the table surface and foam pads were installed under the hinges, allowing the manipulandum to be moved everywhere on the table with minimal inertia and friction.

Two potentiometers (1000 Hz) positioned in the joints of the manipulandum allowed us to measure the angle of each segment, from which the *X*- and *Y*-kinematics of the stylus were estimated. This information was then used to project a cursor corresponding to participants' hand in real time (green circle of 1-cm diameter). The time necessary to collect the *X*- and *Y*-kinematics and present the corresponding visual cursor was estimated to be around 7–9 ms.

Three visual targets (full circles of 1-cm diameter) were presented at a distance of 20 cm from the starting