ELSEVIER

Error-related modulations of the sensorimotor post-movement and foreperiod beta-band activities arise from distinct neural substrates and do not reflect efferent signal processing

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A B S T R A C T

While beta activity has been extensively studied in relation to voluntary movement, its role in sensorimotor adaptation remains largely uncertain. Recently, it has been shown that the post-movement beta rebound as well as beta activity during movement-preparation are modulated by movement errors. However, there are critical functional differences between pre- and post-movement beta activities. Here, we addressed two related open questions. Do the pre- and post-movement error-related modulations arise from distinct neural substrates? Do these modulations relate to efferent signals shaping muscle-activation patterns or do they reflect integration of sensory information, intervening upstream of the motor output? For this purpose, first we exploited independent component analysis (ICA) which revealed a double dissociation suggesting that distinct neural substrates are recruited in error-related beta-power modulations observed before and after movement. Second, we compared error-related beta oscillation responses observed in two bimanual reaching tasks involving similar movements but different interlimb coordination, and in which the same mechanical perturbations induced different behavioral adaptive responses. While the task difference was not reflected in the post-movement beta rebound, the pre-movement beta activity was differently modulated according to the interlimb coordination. Critically, we show an uncoupling between the behavioral and the electrophysiological responses during the movement preparation phase, which demonstrates that the error-related modulation of the foreperiod beta activity does not reflect changes in the motor output from primary motor cortex. It seems instead to relate to higher level processing of sensory afferents, essential for sensorimotor adaptation.

1. Introduction

Modulation of human EEG beta (15–30 Hz) oscillations in relation to voluntary movement was reported several decades ago (Neuper and Pfurtscheller, 1996). However, the functional significance of beta activity in relation to movement-error processing and sensorimotor adaptation processes is still uncertain. Tan et al. (2014) first demonstrated that the beta rebound, an increase in beta power typically observed at the end of movement, is modulated by kinematic errors. Using a hand-controlled-joystick task, they observed that the beta rebound was attenuated for movements in which movement-execution errors were induced by a visual perturbation. Moreover, they demonstrated that this effect was stronger when the context enhanced the salience of the

kinematic errors and proposed that the beta rebound signals neuronal activity implementing Bayesian inference to update internal models during sensorimotor adaptation (Tan et al., 2014). More precisely, it would index the estimation uncertainty, inherent to the forward internal model, about the sensory consequences of the motor-command (Tan et al., 2016).

In a whole-arm reaching task, together with the beta rebound at the end of perturbed trials, we examined beta activity during the preparation (foreperiod) of reaches directly following a perturbed trial (Torrecillos et al., 2015). In contrast to the gradual decrease in beta power immediately preceding movement initiation, which has been extensively described (Nagamine et al., 1996; Pfurtscheller and Lopes da Silva, 1999; Taniguchi et al., 2000; Paradiso et al., 2004), only a limited number of

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studies have examined beta activity further back in time during the foreperiod (for a review see Kilavik et al., 2013). However, several studies using pre-cueing paradigms have reported intermittent beta peaks during the foreperiod between the warning and the imperative cues (Alegre et al., 2004, 2006; Molnár et al., 2008; Fischer et al., 2010; Van Wijk et al., 2009; Zaepffel et al., 2013), and suggested a link between beta oscillations and motor planning in the foreperiod (for a review, see Kilavik et al., 2013). In our previous study (Torrecillos et al., 2015) we contrasted oscillatory responses evoked by two types of reach errors: errors that trigger trial-to-trial motor-command update and errors that do not elicit sensorimotor adaptation. We found that the post-movement beta rebound was similarly attenuated for both types of errors, whereas in contrast the foreperiod beta activity was sensitive to the nature of the perturbation. Specifically, the transient beta power enhancement, peaking around 1 s before movement onset, was attenuated before reaches that followed a movement-execution error activating sensorimotor adaptation, but not after a perturbation that did not trigger trial-to-trial motor-command update. On the basis of these distinct patterns, we proposed that the attenuation of the beta rebound reflects error-salience processing independent of sensorimotor adaptation. In contrast, the modulation of the foreperiod beta power seems to relate to adaptive processes activated after a movement-execution error is experienced.

While they uncover critical functional differences, these findings leave unresolved two central and related issues. First, it remains unknown whether the same or different neural substrates are involved in the pre- and post-movement error-related oscillatory responses. In general, power modulations in brain oscillations may be related to the degree of spike synchronization (Denker et al., 2011) and/or the overall level of activity in neuronal populations (Nauhaus et al., 2009). It has been shown that beta oscillations can synchronize over large networks, spanning multiple cortical (Brovelli et al., 2004; Murthy and Fetz, 1992, 1996; Roelfsema et al., 1997) and sub-cortical (Courtemanche and Lamarre, 2005; Courtemanche et al., 2003) areas. Therefore sensorimotor beta power modulations may reflect different neuronal populations and/or network states. Second, our previous findings do not provide any insight into the nature of the adaptive processes that are reflected by the foreperiod beta modulation. Traditionally sensorimotor beta activity has been considered in relation to descending motor signal functions, but beta oscillations are also prominent in somatosensory areas (Pfurtscheller and Lopes da Silva, 1999; Crone et al., 1998; Cheyne et al., 2003; Brovelli et al., 2004; Van Ede et al., 2010, 2011; 2012; Witham et al., 2007; Lebar et al., 2017). Our results (Torrecillos et al., 2015) do not tell whether the foreperiod beta modulation relates to efferent signals shaping the motor output or to mechanisms involved in the processing and integration of sensory information, critical for the adaptive update of the forthcoming movement (Krebs et al., 1998; Pavlides et al., 1993; Vidoni et al., 2010; Ostry and Gribble, 2016; Mathis et al., 2017).

In order to address these two connected issues, we used two complementary approaches. First, we exploited temporal independent component analysis (ICA) (Makeig et al., 1997; Delorme et al., 2012) to investigate the sources of the pre- and most-movement beta modulations. We used ICA to separate EEG activity into independent components (ICs) on which we performed time-frequency analyses. The patterns of beta-power modulations of relevant ICs, as well as the results of source analyses strongly suggest that distinct neural substrates underlie the modulations of the foreperiod and post-movement beta activities in response to kinematic errors.

Second, as a means of disentangling low-level efferent processes from higher-level information-integration processes, we contrasted bimanual reaching tasks involving physically similar movements but different action goals. The neural control of movement has been extensively studied using unimanual tasks or bimanual tasks involving bilateral separate, symmetrical or reciprocal, movements (Kelso et al., 1979; Marteniuk et al., 1984; Fowler et al., 1991; Donchin et al., 1998; Swinnen, 2002;

McCombe Waller and Whitall, 2008; Liuzzi et al., 2011). In contrast, cooperative tasks in which both hands have to achieve a common goal together have been rarely studied (for review, see Obhi, 2004). In a recent EEG study, Rueda-Delgado et al. (2017) examined changes in beta activity with task difficulty during a bimanual visuomotor task in which participants had to use both hands to draw a line, by rotating two dials (one with each hand) simultaneously. The difficulty of the task was manipulated through the ratio between the dial-rotation speeds. Against their expectations based on previous studies restricted to non-cooperative movements, Rueda-Delgado et al. (2017) found that only sensorimotor regions in the non-dominant right-hemisphere showed a modulation of beta power as a function of task difficulty. These results indicate that extending observations to cooperative movements offer an avenue to dissociate beta activity related to low-level efferent signals from beta activity related to higher-level information-integration processes.

Here, we contrasted beta oscillatory responses to movement errors in two bimanual reaching tasks involving physically similar movements, but different task goals. In a *Parallel* task, participants had to control two independent cursors (each with one hand) to reach simultaneously two different targets. In a *Cooperative* task, they controlled a single cursor with both hands to hit a unique target. In both cases, identical unilateral mechanical perturbations (force-field) were unexpectedly applied to one of the arms in a minority of trials (catch-trials), which elicited different patterns of trial-to-trial motor-command update, depending on the nature of the interlimb coordination. Consistent with the idea that it reflects adaptive processes, we found that the foreperiod beta activity was differently modulated in the two bimanual tasks. In contrast, the post-movement beta rebound exhibited no sensitivity to the nature of the interlimb coordination. More critically, we show that the foreperiod beta modulation does not relate to efferent signals shaping the motor output, but instead relates to upstream mechanisms likely involved in the integration of sensory information, essential for the adaptive updating of the upcoming movement.

2. Material and methods

2.1. Participants

A total of 15 healthy volunteers (9 males and 6 females, mean age 24.8 years, SD = 3.9) took part in the study. All participants were right-handed, as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971) and all had normal or corrected-to-normal vision. All of them were free of neurological or psychiatric disorders and gave informed consent according to a protocol approved by the Ethics Board of the Aix-Marseille University.

2.2. Experimental setup

All tasks were performed using a robotic exoskeleton (KINARM, BKIN Technologies) that allows upper-limb movements in the horizontal plane and permits the application of mechanical loads to the elbow and shoulder joints (Fig. 1A). Participants were seated with both arms installed in the bilateral exoskeleton; the height of the chair was adjusted so that the shoulders were abducted by ~70°. Using a semi-silvered mirror, direct vision of the arms was prevented throughout the task. One or two cursors (depending on the task) projected onto the same plane as the (not visible) hands provided movement visual feedback. Participants hold their hands in a fist, and the position of the cursor was determined by the position of the index knuckle. Head movements were limited by using a chin rest.

2.3. Tasks

Participants had to perform reaching movements to one or two visual targets depending on the task. In the initial configuration, the elbows