Neural oscillations reflect latent learning states underlying dual-context sensorimotor adaptation

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ABSTRACT

Recent studies have suggested that individuals can form multiple motor memories when simultaneously adapting to multiple, but oppositely-oriented perturbations. These findings predict that individuals detect the change in learning context, allowing the selective initialization and update of motor memories. However, previous electrophysiological studies of sensorimotor adaptation have not identified a neural mechanism supporting the detection of a context switch and adaptation to separate contexts. Here, we tested the hypothesis that such a mechanism is identifiable through neural oscillations measured through EEG. Human participants learned to manipulate an object in two opposite contexts (mass distribution). This task was designed based on previous work showing that people can adapt to both contexts. We found that sensorimotor α and β, and medial frontal θ frequency bands all exhibited different response patterns with respect to the error in each context. To determine whether any frequency's responses to error were distinctly related to a switch in context, we predicted single-trial EEG data from a computational learning model that can adapt to multiple contexts simultaneously based on a switching mechanism. This analysis revealed that only medial frontal θ was predicted by a component of the model state that adapts to errors based on a context switch. In contrast, α and β were predicted by a model state that was updated from performance errors independent of the context. These findings provide novel evidence showing that sensorimotor and medial frontal oscillations are predicted by different adaptation processes, and that changes in medial frontal activity may indicate the formation of motor memories by responding to changes in learning context.

1. Introduction

When movements are adapted to one perturbation through errors, e.g., force fields (Shadmehr and Mussa-Ivaldi, 1994), visuomotor rotations (Krakauer, 2009), or a novel object's dynamics (Ingram et al., 2011; Zhang et al., 2010; Witney et al., 2000), then subsequently adapted to an opposite perturbation, adaptation to the first context interferes with adapting to the second (Caithness et al., 2004; Krakauer, 2009; Miall et al., 2004). This phenomenon is often evidenced by slower adaption to the second perturbation compared to the first context, i.e., anterograde interference (Brashers-Krug et al., 1996; Smith et al., 2006; Wolpert et al., 2011). These findings are thought to arise from the motor memory for the first context competing with learning of the second context, wherein adaptation to the second context is assumed to overwrite adaptation to the first context (Caithness et al., 2004; Krakauer et al., 2005; Miall et al., 2004; Sing and Smith, 2010; Smith et al., 2006).

Despite extensive findings of interference between similar perturbations, several studies have shown people can simultaneously adapt to two opposing perturbations (Fu and Santello, 2015; Hirashima and Nozaki, 2012; Imamizu et al., 2007; Lee and Schweighofer, 2009; Nozaki et al., 2016; Sheahan et al., 2016). This finding implies that previously learned motor commands for one context are at least partially protected during learning of a novel, but related perturbation context (Pekny et al., 2011). Another implication of this work is that individuals form context-dependent motor memories (Lee and Schweighofer, 2009). The formation of context-dependent motor memories further predicts that individuals detect a change in perturbation context through either explicit (Miall et al., 2004; Osu et al., 2004) or implicit cues, such as an unexpected increase in error (Lee and Schweighofer, 2009). In fact, Lee and Schweighofer (2009) demonstrated that augmenting a two-timescale learning model could account for scenarios wherein individuals could adapt to and recall the appropriate motor commands for distinct

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perturbation contexts. The novelty of their approach was allowing the model to switch and adapt different learning states depending on the perturbation context. The model consists of two processes: one that learns quickly from errors (*fast* state) and one that learns slowly (*slow* state) (Smith et al., 2006). Furthermore, the slowly-adapting states support adaptation to multiple contexts because they are only updated from errors experienced in their respective context. In contrast, fast states are always updated from error in a context-independent fashion.

While behavioral evidence indicates that individuals can adapt to one or multiple perturbation contexts simultaneously, it remains an open question what neurophysiological mechanisms instantiate processes such as the gating of adaptation to changes in context. We propose that these mechanisms can be identified by examining neural oscillations. This proposition is based on accumulating evidence from electroencephalography (EEG), magnetoencephalography (MEG), and local field potential (LFP) studies showing different frequencies convey informational content underlying necessary computations involved in learning, including forming sensory predictions, error processing, and weighting of errors (Arnal and Giraud, 2012; Cavanagh et al., 2009; Cohen et al., 2011; Contreras-Vidal and Kerick, 2004; Friston et al., 2015; Sedley et al., 2016; Tan et al., 2016). In the present study, we chose to focus on sensorimotor α and β, and medial frontal θ frequencies because they have implicated as being sensitive to error-processing during sensorimotor adaptation (Arrighi et al., 2016; Contreras-Vidal and Kerick, 2004; Tan et al., 2014, 2016).

We tested the overarching hypothesis that different neural frequencies that are responsive to sensorimotor error would index context-dependent and -independent states posited in dual-context learning models (Lee and Schweighofer, 2009). Based on previous work (Arrighi et al., 2016; Cavanagh et al., 2010; van de Vijver et al., 2011; Womelsdorf et al., 2010), we expected that medial frontal θ would represent the processing of performance errors in a context-dependent fashion. We were also interested in whether or not this θ context-dependent relation would index the initiation of a new learning context or reflect an overall sensitivity to switching between learning contexts. Although sensorimotor α and β have been identified in adaptation studies, there is still no consensus on the role they play in error processing and learning (Gentili et al., 2011; Tan et al., 2014). Therefore, an additional goal of this study was to further elucidate the role of these frequencies in sensorimotor adaptation. We tested these hypotheses by combining a task involving dexterous object manipulation (Zhang et al., 2010), EEG, and an error-based learning model (Lee and Schweighofer, 2009).

2. Materials and methods

2.1. Participants

Twenty-five participants aged 20–29 years (18 males) with normal to corrected vision and no history of neurological disorders were recruited for participation. All participants were right-handed (self-reported). All individuals provided written informed consent prior to testing in accordance with the Declaration of Helsinki. The procedures were approved by the Office of Research Integrity and Assurance at Arizona State University.

2.2. Apparatus

The apparatus and manipulation task have been described in detail in our previous work (Fu et al., 2010; Zhang et al., 2010). Briefly, participants were asked to reach for and lift an inverted T-shaped object (Fig. 1A). The object has 3 hidden bottom compartments that were used to place a metal weight (400 g). View of the location of the added mass was blocked by an opaque lid to prevent subjects from using visual cues to anticipate the external torque. Note that Fig. 1A shows the mass as visible only for graphical purposes. Changing the weight's compartment (left, center, or right) alters the object's center of mass (CM). When the
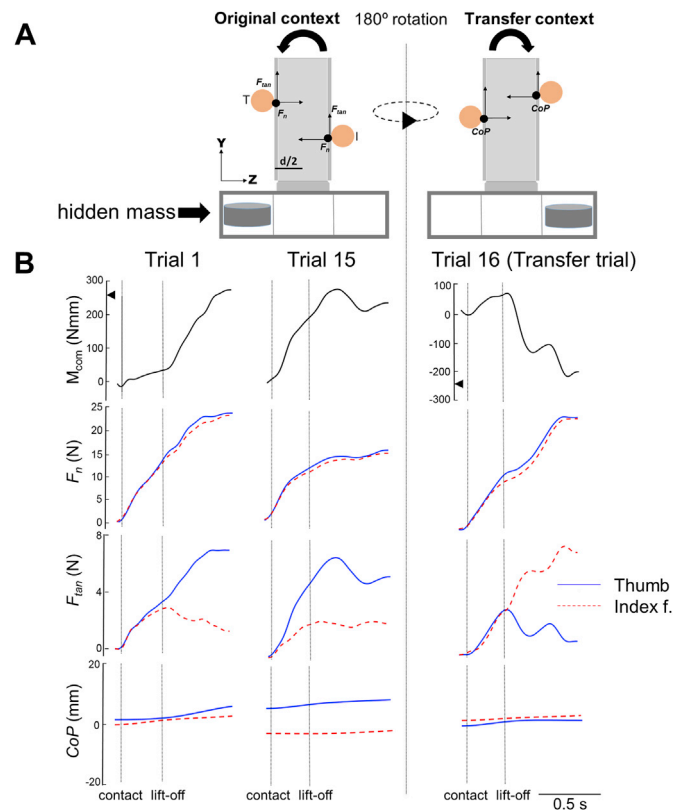

Fig. 1. *Grip device and representative behavioral data. A: Grip device instrumented with force/torque (F/T) sensors.* Participants grasped and lifted the device with the thumb and index fingertips (denoted by T and I, respectively). F/T sensors measured normal and tangential forces (F_n and F_{tan}, respectively), and allowed computing digit (filled circle) center of pressure (CoP) on the grasp surface (height: 94.6 mm). The figure also shows the variable "d/2" used for computing the compensatory moment (M_{com}). The object bottom consists of compartments to place a mass (400 g) to generate a (counter-)clockwise torque (denoted by black arrow). Participant's vision of the added mass was blocked by a cover. In the figure, the mass is visible only for graphical purposes. The grip device is shown before and after a 180° rotation around the vertical axis. In the example, object rotation changes the external torque direction from counterclockwise to clockwise. B: From top to bottom, data shown are M_{com}, F_n and F_{tan} exerted by thumb and index finger (solid and dashed lines, respectively), and CoP of each digit. Participants performed a 180° rotation of the object without lifting it to switch task context. Data are from trials 1 and 15 prior to object rotation (Original context), and the first transfer trial (trial 16, or first Transfer context trial), performed by a representative subject. The arrow inside the M_{com} plots denotes the counterclockwise external moment (Original context), and the clockwise external moment following object rotation (Transfer context). From left to right, vertical lines within each column of plots denote onset of grip forces and object lift-off, respectively.

mass was placed on the left or right compartment, it created an external moment (-255 and $+255$ Nmm, respectively) acting to rotate the object on the frontal plane. The object has two vertical panels that allow participants to grasp anywhere on the object's sides. Forces and moments exerted by each digit on the panels were measured using two six-component force/torque (F/T) transducers (Nano 17, ATI Industrial Automation, Garner, NC; nominal force resolution: 0.012 N; nominal torque resolution: 0.63 N cm). These forces correspond to the normal and tangential (vertical) forces produced by each digit on each plate placed over each force sensor (sampling rate: 1 kHz). We used an LCD monitor (60 Hz refresh rate), placed behind the object, to display the 'ready' and 'go' signals on each trial (see *Experimental protocol* below). The monitor was adjusted to each individual's eye height. A hand switch was placed at a fixed distance of 10 cm from the object and was used to detect reach onset. The switch was oriented such that the participant's hand posture was aligned with the grasping posture on the object to minimize the need for wrist flexion or extension for grasping. A second switch was placed beneath the object and was used to determine object lift-off.

EEG data was recorded using a 64-channel Acticap system