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Arm-use dependent lateralization of gamma and beta oscillations in primate medial motor areas

Ryosuke Hosaka [a,b], Toshi Nakajima [c,d], Kazuyuki Aihara [e], Yoko Yamaguchi [b], Hajime Mushiake [c,d,*]

[a] Department of Applied Mathematics, Fukuoka University, Fukuoka 814-0180, Japan
[b] Neuroinformatics Japan Center, RIKEN Brain Science Institute, Wako 351-0198, Japan
[c] Department of Physiology, Tohoku University School of Medicine, Sendai 980-8575, Japan
[d] Core Research for Evolutional Science and Technology (CREST), Japan Science and Technology Agency, Kawaguchi 332-1102, Japan
[e] Institute of Industrial Science, The University of Tokyo, Tokyo 153-8505, Japan

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ABSTRACT

The neurons in the motor cortex show lateralization depending on the arm to use. To investigate if local field potential (LFP) oscillations change with contralateral and ipsilateral arm use, we analyzed the power of LFP in supplementary motor areas (SMA) and pre-SMA while animals performed a delayed-response arm use task under visual guidance and memory-based. LFP power changed with the laterality of the arm use, but it was frequency dependent. Specifically, power in the gamma range increased during contralateral arm use, while beta power increased with ipsilateral arm use. Subsequently, we confirmed that the frequency-dependent laterality was true also for the memory-driven movements. Our data therefore suggest that gamma oscillation is linked to the local neuronal activities in the contralateral hemisphere, and beta oscillation is related to withholding undesired arm movements by suppression of the local neuronal activities of the ipsilateral hemisphere.

1. Introduction

Neuronal activity in the motor cortex alters in relation to the laterality of the effector (Tanji, Okano, & Sato, 1988). Over 80% of primary motor cortex neurons increase activity before and during movements performed using the contralateral effector. In the premotor cortex, the contralateral and ipsilateral neurons constitute 13% and 9% of total neurons, respectively. In the medial motor area [such as the supplementary motor area (SMA) and pre-SMA], 31% of neurons are contralateral neurons, and only 4% neurons are ipsilateral neurons. As such, movement representation is lateralized in the lateral and medial motor cortices.

Populations of neurons co-activate repeatedly for short temporal epochs, resulting in synchronized oscillation expressed by unit activity and local field potentials (LFP) (Buzsáki, Anastassiou, & Koch, 2012). Oscillations of LFPs include several distinct frequency bands (Buzsáki, 2009). The beta oscillation (10–40 Hz) is the most studied oscillatory phenomenon throughout the primate motor system (Baker, Olivier, & Lemon, 1997; Donoghue, Sanes, Hatsopoulos, & Gaál, 1998; Murthy & Fetz, 1992; Sanes & Donoghue, 1993). This oscillation reflects motor preparation, and it is attenuated during motor execution (Donoghue et al., 1998; Sanes & Donoghue, 1993) and during motor imagery without exact effector movement (Gilbertson et al., 2005; Kühn et al., 2006). Beta oscillations are also involved in the maintenance of motor or postural sets (Engel & Fries, 2010). Furthermore, beta-range cortico-muscular coherence has been documented during static force output (Gwin & Ferris, 2012).

The gamma oscillation (>40 Hz) has captured the most attention recently. In the motor cortex, gamma oscillations have been implicated in motor execution (Pfurtscheller, Neuper, & Kalcher, 1993). They have also been shown to mediate cortico-spinal interactions (Schoffelen, Oostenveld, & Fries, 2005). The cortico-muscular coherence in the gamma range has been linked to dynamic force output (Gwin & Ferris, 2012).
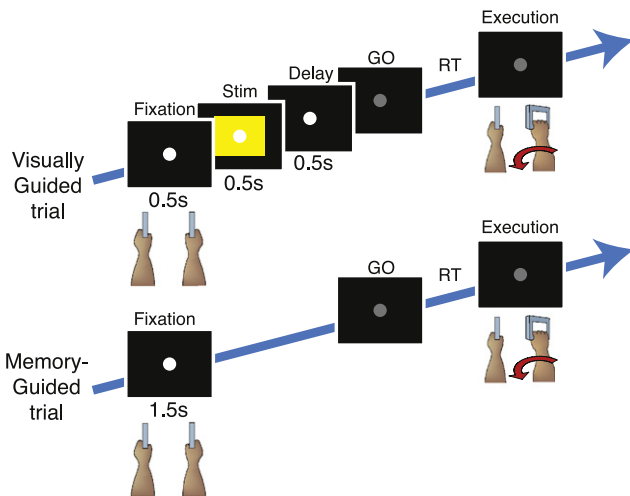
Fig. 1. The sequence of events in the task. Top: example of a trial in which the animals were required to perform a movement in accordance with a cue (visually guided trial). The monkey was required to memorize a particular movement (right forearm pronation–left forearm pronation in this example) while performing the visually guided trials three times. Bottom: memory-guided trials in which the movement was memorized; only GO signals were given. For both types of trials, the monkey gazed at the central fixation point on the screen during the initial 500 ms period.

Although EEG and MRI studies revealed lateralization of oscillatory activity of the lateral motor cortex, the laterality in the medial motor cortex is less well defined because the spatial resolutions of the EEG and MRI are too broad to accurately separate left and right medial motor cortices. We therefore examined the lateralization of beta and gamma oscillations in the medial motor cortex using the LFP of the SMA and pre-SMA.

2. Methods

Two Japanese monkeys (*Macaca fuscata*, M and N, 6.5 and 5.8 kg) were used and were cared for in accordance with the Guiding Principles for the Care and Use of Laboratory Animals of the National Institutes of Health. During experimental sessions, the monkeys were seated in a primate chair facing a screen. The monkeys held manipulandums in both forelimbs and were trained to perform a delayed-response forelimb movement task (Fig. 1 upper part). Trials started with the presentation of a white spot of light (fixation point) in the center of a screen, which the monkeys fixated on. They were then required to place the manipulandums in a neutral position. After a 500 ms holding period, one of four colored squares appeared on the display to instruct the monkeys to perform supination or pronation of either forelimb. After another 500 ms waiting period, a "GO" signal was displayed, prompting the monkeys to perform the movement as instructed.

The task block was consisted of the six trials. The first three trials in a block were performed under visual guidance of instructional cues (visually guided trial). For the remaining three trials in the block, the animal performed the movements instructed in the previous visually guided trials with no visual cue (memory-guided trials, Fig. 1 lower part).

To record the LFPs, a single-site electrode, with an impedance of 0.5–2 M Ω, was inserted into the left or right side of the pre-SMA or SMA while the monkeys performed the task (Fig. 2) (Matsuzaka, Aizawa, & Tanji, 1992). The epochs of the LFP were filtered (5–300 Hz) and digitally sampled (at 1 kHz), starting from the fixation point and lasting until 500 ms after the GO signal.
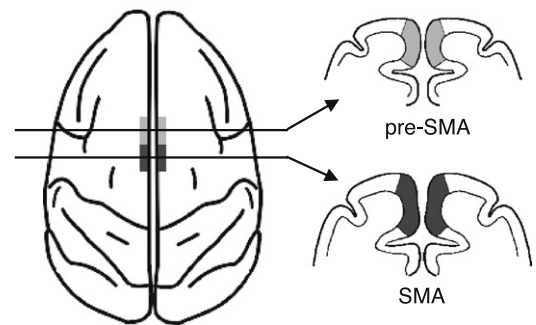

Fig. 2. Schematic drawing of the recording sites. Recording sites in the medial cortex are illustrated in the coronal sections obtained at two rostro-caudal levels (color-coded), as drawn on the cortical surface map.

For spectral analysis of the LFPs, we used customized versions of Matlab and R code. The time–frequency power of each LFP was obtained by a wavelet transformation with the Gabor mother wavelet as follows:

$$w(t, f_0) = g(t)\{\exp(i2\pi f_0 t) - \exp(-\sigma^2 (2\pi f_0)^2)\},$$

$$g(t) = \frac{1}{2\sigma \sqrt{\pi}} \exp\left(\frac{-t^2}{4\sigma^2}\right),$$

where t is the time, f_0 is the central frequency, and $\sigma = 5/f_0$. By convolving the mother wavelet to the LFP time series $S(t)$, the LFP power $E(t, f)$ at the electrode was computed. The moment-to-moment oscillatory power was expressed as a z-score with respect to the average and the standard deviation of the power during the baseline 500 ms fixation periods.

3. Results

The monkeys performed the appropriate movements in response to the visual instructions, and LFPs were recorded in the pre-SMA and SMA during the behavioral task. A total of 57 sessions were recorded in the pre-SMA and 51 in the SMA for monkey M, and 345 were analyzed in the pre-SMA and 191 in the SMA for monkey N. Fig. 3(A–B) shows examples of LFP activities simultaneously recorded in the (A) pre-SMA and (B) SMA. The LFPs of the pre-SMA and SMA covaried. The correlation coefficient of this example was 0.289 (0.400 in a single example session).

Fig. 3(C–F) shows the time–frequency plots of an average of the LFP power of monkey M in the visually guided trials (C–D) and in the memory-guided trials (E–F). The LFP power in each trial was normalized by the power during the initial 500 ms (0 to 500 ms from fixation). In the visually guided trial of the pre-SMA (Fig. 3(C)), gamma power increased phasically during the stimulus presentation and after the GO signal (red triangle and red arrow). In addition, beta power decreased concurrently with the increase in gamma power (blue triangle and arrow). In the visual trial of the SMA (Fig. 3(D)), the increase in gamma power was not observed during stimulus presentation and weakly occurred after the GO signal. The beta power decreased during the stimulus presentation and after the GO signal (blue triangle and arrow). In the memory-guided trials of both areas (Fig. 3(E–F)), the gamma power increased and beta power decreased after the GO signal (red and blue arrows, respectively). In addition, the beta power persistently increased during the preparation period (red horizontal bar).

To examine if the power of the LFP oscillations changed according to the arm used, we used the Welch t-test to compare the LFP