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

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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 that 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.

Keywords: Local Field Potential, Supplementary motor area
1. Introduction

Neuronal activity in the motor cortex alters in relation to the laterality of the effector (Tanji et al., 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 laterialized 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 et al., 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 (Murthy and Fetz, 1992; Sanes and Donoghue, 1993; Baker et al., 1997; Donoghue et al., 1998). This oscillation reflects motor preparation, and it is attenuated during motor execution (Donoghue et al., 1998; Sanes and Donoghue, 1993) and during motor imagery without exact effector movement (Kühn et al., 2006; Gilbertson et al., 2005). Beta oscillations are also involved in the maintenance of motor or postural sets (Engel and Fries, 2010). Furthermore, beta-range cortico-muscular coherence has been documented during static force output (Gwin and 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 et al., 1993). They have also been shown to mediate cortico-spinal interactions (Schoffelen et al., 2005). The cortico-muscular coherence in the gamma range has been linked to dynamic force output (Gwin and Ferris, 2012).

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 manupilandums 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 monkey to perform supination or pronation of either forelimb. After another 500-ms waiting period, a “GO” signal was displayed, prompting the monkey 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 (Matsuzaka et al., 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.

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 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. Figure 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 single example session).

Figures 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 visually guided trial of the pre-SMA (Fig. 3C), 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 visual trial of the SMA (Fig. 3D), 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. 3E-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 Welch t-test to compare the LFP power with ipsilateral and contralateral arm use. Firstly, we analyzed LFPs of the visually guided trials. The time-frequency plots of power differences with arm use are shown in Fig. 4A and B. Thick horizontal lines indicate the period of stimulus presentation, and the color codes indicate the regions where oscillations were significantly stronger for either ipsilateral (red) and contralateral arm use (blue). Beta and gamma oscillations showed different lateralization according to the arm use. Specifically, gamma power was significantly stronger when monkeys were about to perform a movement with the contralateral arm compared with the ipsilateral arm (p < 0.01), whereas beta power was significantly stronger with ipsilateral arm use (p < 0.01). The significant regions of the pre-SMA were broadly distributed, whereas the distribution
in the SMA was biased to the period immediately following the GO signal. Interestingly, the distribution bias of beta power resembled that of gamma power.

The areas of significance are summarized in Fig. 4C, D. To evaluate the effects of movement preparation and movement execution on lateralization, the trial was separated into two periods: early (from stimulus onset to 250 ms after the termination of the stimulus), and late (from 250 ms after termination of the stimulus until 500 ms after the GO signal). In the gamma frequency range, the total area (a sum of the early and late periods) was larger for use of the contralateral arm compared with the ipsilateral. In contrast, the total area for the ipsilateral arm use was larger than the contralateral in the beta frequency range. In the SMA, the area of the late period is larger than that of the early period in both the beta and gamma frequency bands, which was not observed in the pre-SMA.

Then, we tested if the power of the LFP oscillations changed according to the arm used also under the memory-guided conditions. The result was shown in Fig. 5. As the same with the visually-guided trials, beta and gamma oscillations showed different lateralization according to the arm use.

4. Discussion

We carried out LFP recordings from primate bilateral pre-SMA and SMAs, and found that beta and gamma frequency bands change the lateralization of LFP power in the medial motor cortex. In general, the power of the gamma oscillation increased with contralateral arm use, whereas beta power was augmented during ipsilateral arm use. Specifically, the laterality of the beta and gamma oscillations was distinct during the preparation period in the pre-SMA, and during the execution period in both the pre-SMA and SMA. These results suggest that the gamma and beta oscillations in the SMA is crucial for the movement execution, and the oscillations in the pre-SMA play a role in also the movement preparation.

Gamma oscillations are closely related to neuronal spikes, and as such they frequently exhibit simultaneous activation (Fries et al., 2007). Gamma oscillation may therefore co-operate with neuronal activities to select an appropriate effector for movement (Fig. 6). In contrast, beta power increased during ipsilateral movement. The maintenance of beta oscillation during ipsilateral movement implies that beta oscillation is involved in withholding the undesired arm movement. Moreover, bilateral pre-SMAs and SMAs
are inter-connected through corpus callosum. The enhanced beta oscillation might mediate inter-hemisphere information transmission.

One of the major roles of the brain oscillation is to mediate communications inside the brain. Although the pre-SMA and SMA have different roles in the motor planning, the LFPs of these two areas are weakly synchronized (Fig.3). So, the signals of the pre-SMA and SMA might interact through oscillations. The gamma and beta oscillations are strong candidates of the career of the inter-areal communications. Coherence analysis between the pre-SMA and SMA will reveal the roles of the oscillations on the inter-areal communications.

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References


Figure 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.

Figure 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.
Figure 3: Examples of the LFP activity. (A-B) Raw LFPs simultaneously recorded from the (A) pre-SMA and (B) SMA in the left hemisphere of monkey N. The traces were recorded during the visually guided 1st trial. The horizontal thick bar indicates 500 ms. The vertical thick bar indicates 0.05 mV. (C-F) Time frequency plots of the average of the power of LFP in the pre-SMA (C,E) and SMA (D,F) of monkey M during visually guided (C,D) and the memory-guided trials (E,F). The LFP activity was normalized by power during the 0-500 ms after the fixation. The colors indicate the z-score of the power: red horizontal bar, triangles and arrows indicate the activation of gamma power, whereas blue triangles and arrows indicate the suppression of beta power. Thick horizontal black lines indicate the period of stimulus presentation.
Figure 4: (A-B) Time-frequency plots of power differences compared with arm use in pre-SMA and SMA in two monkeys. Color codes indicate the regions where the gamma oscillations were significantly stronger ($p < 0.01$) for ipsilateral (red) and contralateral arm use (blue). Thick horizontal lines indicate the period of the stimulus presentation. (C-D) The area of the time-frequency region showing lateralization for ipsilateral (red) and contralateral arm use (blue). The areas for the early and late periods are depicted by the light and dark colors, respectively. The area was represented by a ratio of the entire region (from stimulus onset to 500 ms after the GO signal). M and N represent monkey M and N, respectively. (C) The laterality of the gamma oscillation. (D) The laterality of the beta oscillation.
Figure 5: (A-B) Time-frequency plots of power differences compared with arm use in pre-SMA and SMA in two monkeys under memory-guided trials. The basic format is the same with the Fig.4.

Figure 6: Reciprocal role of gamma and beta oscillation in arm use selection.