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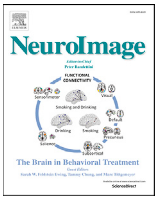

Temporal recalibration of motor and visual potentials in lag adaptation in voluntary movement

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ABSTRACT

Adaptively recalibrating motor-sensory asynchrony is critical for animals to perceive self-produced action consequences. It is controversial whether motor- or sensory-related neural circuits recalibrate this asynchrony. By combining magnetoencephalography (MEG) and functional MRI (fMRI), we investigate the temporal changes in brain activities caused by repeated exposure to a 150-ms delay inserted between a button-press action and a subsequent flash. We found that readiness potentials significantly shift later in the motor system, especially in parietal regions (average: 219.9 ms), while visually evoked potentials significantly shift earlier in occipital regions (average: 49.7 ms) in the delay condition compared to the no-delay condition. Moreover, the shift in readiness potentials, but not in visually evoked potentials, was significantly correlated with the psychophysical measure of motor-sensory adaptation. These results suggest that although both motor and sensory processes contribute to the recalibration, the motor process plays the major role, given the magnitudes of shift and the correlation with the psychophysical measure.

Introduction

To achieve an intentional goal, we usually need to perform a series of adaptive actions in voluntary movement. Every action has a subsequent outcome, and adaptively and precisely synchronizing the outcome with the action is essential for all living animals. For example, a moving animal must distinguish the sound of its walking from environmental sounds in order to remain alert to nearby predators (Stetson et al., 2006). This synchrony may be confounded by changes of delay in motor circuits (e.g., fatigue) or sensory circuits (e.g., slow response of mouse cursor due to computer overload), and the brain must continuously recalibrate such asynchrony. Adaptation to a motor-sensory lag, in which the perceived time between an action and a delayed consequence is compressed after repeated exposures to the delay, is an example of such recalibration (Haggard, 2005; Stetson et al., 2006).

In voluntary movement, it is controversial whether the recalibration resulting from sensory lag adaptation occurs in sensory or motor circuits. One theory hypothesizes that the perceived timing of a sensory event shifts earlier to the timing of an action in delay condition than in no-delay condition (Cai et al., 2012; Stetson et al., 2006). This theory is based on an illusory reversal of action and outcome: Participants perceive that sensory events occur before their actions when the delay is unexpectedly removed after the adaptation. This suggests the importance of calibration in sensory circuits after sensory events (retrospective processes).

Another theory suggests the importance of prospective processes within motor-related circuits (Haggard, 2014). This is supported by findings that outcome predictability (Haggard et al., 2002; Moore and Haggard, 2008) prior to the action is necessary for the 'intentional binding' effect (Haggard et al., 2002), which refers to the subjective compression of an interval between a voluntary action and a delayed

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outcome. Another psychophysical study reported a transfer of adaptation effect between motor-visual and motor-auditory asynchrony, suggesting the motor system's involvement in lag adaptation (Sugano et al., 2010).

However, to our knowledge, it is unknown which components in a motor-related process change according to the recalibration. Previous studies have suggested that our awareness of movement is derived from signals that precede the movements rather than sensory feedback from a moving limb (Blakemore and Frith, 2003; Libet et al., 1983). Readiness potentials are well-known neural signals that precede movements (Kornhuber and Deecke, 1965; Shibasaki and Hallett, 2006). Moreover, previous studies suggested the importance of Brodmann area (BA) 6 (including premotor and supplementary motor areas) and parietal regions to motor intention (Haggard, 2008; Lau et al., 2004) and preparation (Wheaton et al., 2005). Therefore, we hypothesized that a significant change due to recalibration could be found in the readiness potentials in BA 6 and parietal regions in cases where a prospective process contributes to the recalibration.

To examine this hypothesis, we investigated how readiness potentials, which gradually increase toward the onset of voluntary movement (a button press in this study), change in BA 6 and parietal regions due to lag adaptation. We used MEG for measurement of the magnetic signals related to the readiness potentials and estimated the source cortical currents from the MEG signals in combination with fMRI measurements. We also investigated changes in the retrospective sensory-related circuits. Specifically, we investigated visually evoked potentials whose main sources have been localized in the occipital lobe (BA 17/18/19) (Di Russo et al., 2002). Although previous studies (Di Luca et al., 2009; Keetels and Vroomen, 2008) found changes in tactile and proprioceptive perception in lag adaptation, we mainly investigated changes in visually evoked potentials that are directly related to the delayed sensory consequence (a flash in this study). We found that, although both the prospective motor process and the retrospective sensory process contribute to the recalibration, the motor process preceding the movements in parietal regions seems to play the major role, considering the magnitudes of the shift and the correlation with the psychophysical measure of the adaptation.

Materials and methods

Experimental design

We measured brain activities using MEG while participants voluntarily pressed a button and observed a consequent flash in delay and no-delay conditions (see Supplementary Fig. 1 for a graphical overview of our experimental design). fMRI activity in a voluntary button-press task was measured to estimate cortical source currents from the MEG signals. From the estimated cortical currents, we identified readiness currents (corresponding to readiness potentials in electroencephalogram measurement) and estimated temporal shifts of the currents due to a lag adaptation. Temporal shifts of flash-evoked currents (visually evoked currents, corresponding to visually evoked potentials in electroencephalogram measurement) were also estimated within the visual cortex. Next, we tested the statistical significance of shifts in readiness and evoked currents, as well as the correlation between the degree of current shifts and a psychophysical measure of lag adaptation obtained from a temporal order judgment task following the voluntary button-press task.

Participants

Sixteen right-handed male participants (aged 20–45 years, mean 25.1) participated in this study. A signed informed consent form was obtained from each participant. The experiments were conducted according to the Declaration of Helsinki and approved by the Ethics Committee at Advanced Telecommunication Research Institute International (http://www.atr.jp).

Experimental setup for MEG experiment

The MEG experimental setting is shown in Supplementary Fig. 2A. Participants lay supine in a magnetically shielded room. We used a microcontroller system (Arduino Uno R3, SparkFun Electronics, USA) and optical fiber for precise timing control of the flash (see “Measurement of system delay” in Supplementary Methods). Button presses by the right middle, left index, and left middle fingers were recorded to the microcontroller board. Button presses by the right middle finger were also recorded to the MEG system through channels for external devices. A visual stimulus (flash) was produced by a light-emitting diode (LED) attached to the microcontroller, and it was shown to participants via an optic fiber extended to the center of the semi-transparent screen in front of the participant's face in the shielded room. The center of the screen was indicated by a virtual crossing point of three white lines (the “inverted T”; Supplementary Fig. 2B). The line below the crossing point was omitted to save space for showing task instructions (such as “press” and “judgment”). An auditory stimulus was sent to participants through an air tube. White noise was played via an air-tube headphone during the entire experiment to block the sound of button presses so that participants could not perceive the timing of the button presses by listening. Vertical and horizontal electro-oculogram (EOG) data were recorded to detect blinks and eye movements. Electromyogram (EMG) data were recorded from two surface electrodes on the flexor digitorum superficialis (FDS) to detect muscle activities of the right middle finger. In our preliminary experiment, we compared EMG patterns evoked by the index finger to those evoked by the middle finger. We found that onsets of EMG for the middle finger could be more reliably detected than for the index finger. Thus, we asked participants to use the middle finger in our voluntary button-press task (see below).

Tasks for participants in MEG experiment

Voluntary button-press task. Participants were asked to press a button with their right middle finger at their own pace and focus on the flash as the visual feedback of action outcome. The flash appeared as soon as the button was pressed (<0.4 ms, see “Measurement of system delay” in Supplementary Methods) in the no-delay condition (Fig. 1B) or 150 ms after the button press in the delay condition (Fig. 1A). The duration of flash was 50 ms. Participants were not informed about the lag of the flash during the experiment. Participants briefly practiced at pressing the button in random intervals between 5 and 10 s before the experiment.

Temporal order judgment task. For psychophysical measurement of the lag adaptation effect in individuals, voluntary button-press tasks (Fig. 1A and B) were followed by a temporal order judgment task (Fig. 1C). Participants responded to an auditory cue (frequency: 880 Hz, duration: 100 ms) as quickly as possible by pressing the same button with their right middle finger. Then participants reported whether the button press was earlier or later than the flash by pressing one of two buttons with their left index or middle finger. The software kept a running average of each participant's reaction time to the auditory cues given so far, making it possible to probabilistically place flashes just before or after the button press. The flash onsets were determined by a Gaussian distribution centered on 60 ms after the average response time with a standard deviation of 80 ms to maximize the number of trials at the steep part of the psychometric functions (e.g., Fig. 1D). This procedure followed a previous study on recalibration of motor-sensory asynchrony (Stetson et al., 2006).

Procedures of MEG experiment

Supplementary Fig. 3 shows the procedures of the MEG experiment. Before MEG measurement, there were sessions of response time measurement and training of temporal order judgment (Supplementary