

Brain activity on observation of another person's action:

A magnetoencephalographic study

(動作観察時の視点の違いによる脳磁場活動の研究)

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リハビリテーション療法学専攻

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要旨

【背景】

観察した他者の身体部位を自己の身体図式に適応させる役割を担う神経基盤としてミラーニューロンシステム（Mirror Neuron System : MNS）が知られている。しかし、MNSに関連した研究において空間的位置関係に着目した研究は少ない。リハビリテーション場面では、対象者が観察する視点は一定したものに限らず、対象者とセラピストとの位置関係によって空間的認識は異なる。そのため、視点の違いによる認知過程の神経基盤を明らかにすることで、脳病変部位と運動機能障害との関連、リハビリテーションにおける運動教示や訓練方法に関する基礎的知見の提供が可能になると考えた。

【目的】

Magnetoencephalography（MEG）を用い、異なる空間的位置関係から観察した時の脳磁場活動を計測し、動作観察時の空間的視点の違いをコードする神経活動を明らかにすることを目的とした。

【方法】

対象者は健常成人 10 名（ 23.4 ± 1.2 歳）であり、磁気シールドルーム内で全頭型 MEG（PQ1160C）を使用し、対象者の動作観察時、模倣時、静止画観察時の脳磁場をそれぞれ記録した。呈示される動画の視点は、一人称の右手を観察する視点（1P-R）と、他者の右手を観察する視点（2P-R）、一人称の右手の鏡像を観察する視点（Mirror-R）の3つ

とした。予め **region of interest (ROI)** を設定し、**ROI** の皮質間神経活動と皮質内神経活動の機能的連関を明らかにするためにコヒーレンス解析を用いた。

【結果】

θ 、 α 、 $\text{low-}\gamma$ の 3 つの周波数帯域において、視点の違いによる皮質間コヒーレンス値に有意差を認めた。 θ 帯域では、**Mirror-R** に比べ **1P-R** 時に高いコヒーレンス値を示した。 α 帯域においては、**1P-R** 時に **2P-R** より高いコヒーレンス値を示した。一方 $\text{low-}\gamma$ 帯域では **1P-R** に比べ **2P-R** の時に高いコヒーレンス値を示した。皮質内コヒーレンス解析では、静止画観察時に比べ、動作観察、模倣時に有意に高いコヒーレンス値を示した。

【考察】

空間的視点の認識は、異なる皮質間の神経接続によって処理されていることが示唆された。特に前頭葉や運動感覚関連領域の神経活動は、視点の違いにより異なることを示した。また動作観察時には模倣時と相対的に同様の神経活動の変化が認められ、動作観察時は、実際の動作時と類似した神経活動が生じていると考えられた。

Key words : 手指運動、ミラーニューロンシステム、視点、運動学習

Abstract

Brain activity was recorded using a whole-head magnetoencephalography system followed by coherence analysis to assess neural connectivity in ten healthy right-handed adults to clarify differences in neural connectivity in brain regions during action observation from several perspectives. The subjects were instructed to observe and memorize (OB) or imitate (IM) the hand action from a first-person or second-person visual perspective. The brain activity in coherence was modified among frontal and central, sensorimotor, and mirror neuron system (MNS)-related regions based on the visual perspectives of finger movements. The regional activity in coherence changed similarly under the IM and OB tasks compared with the condition of observing static (ST) hand figures. The information from different visual perspectives of body movements was processed in the frontal-central regions related to sensorimotor processes and partially in MNS.

Key words: Hand movement, Mirror neuron system, Visual perspective, Motor learning

1. Introduction

When a person learns a new motor skill, it is crucial to observe the movement performed by another individual (Wulf, Shea, & Lewthwaite, 2010). In such processes, the adaptation of another person's action to one's own body is required (Meltzoff, & Moore, 1977), and the mirror neuron system (MNS) is considered to play a major role in the process (Iacoboni, & Dapretto, 2006). Cortical areas contributing to MNS include the ventral premotor area, F5 in Macaque monkeys (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996), being well-known for neural networks induced on executing a specific action as well as during observing an action performed by another person (Gallese et al., 1996; Umiltà et al., 2001). Multiple regions of the brain have subsequently been associated with MNS in humans, such as the inferior frontal gyrus (IFG), ventral premotor cortex (PMv), inferior parietal lobe (IPL), superior temporal sulcus (STS), primary sensory area (S1), and primary motor area (M1) (Avikainen, Forss, & Hari, 2002; Buccino et al., 2001; Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995; Nishitani, & Hari, 2000; Rizzolatti et al., 1996).

When we observe another's action, interpretation of the action may vary with different visual perspectives, i.e., the relative location of one's own body to the body of the person performing the action. Although there have been numerous studies concerning MNS in

humans, little is known about how MNS is influenced by different visual perspectives. Previous research applied stimuli from a single perspective (Jonas et al., 2007; Montgomery, Isenberg, & Haxby, 2007; Wheaton, Thompson, Syngeniotis, Abbott, & Puce, 2004), e.g., the performer faced or was parallel to the observer. In clinical situations, the relative position between a patient and therapist is important to show motor performance by the therapist, related to the brain lesion of the patient. Therapists often select their relative position to the patients depending on the side of paresis or spatial neglect in the patients. However, it is not clear that therapists should choose their relative position to patients with a specific brain lesion, based on a brain function for viewing from a perspective. In the present study, we clarified the difference in brain activity among visual perspectives when observing another's motor performance. Analysis techniques and knowledge have been developed to interpret neural networks including MNS, mainly in studies using functional magnetic resonance imaging (fMRI) (Buccino et al., 2001; Buccino, Binkofski, & Riggio, 2004). One neural activity responding to specific stimuli was not provoked separately but modulated by interacting with multiple neurons (Mesulam, 1998).

The objective of the present study was to clarify differences in neural connectivity during action observation among several perspectives in brain regions that contribute to motor control and MNS. We used a magnetoencephalography system, which has the advantages of

a high temporal resolution and reliable source estimation (Lounasmaa, Hämäläinen, Hari, & Salmelin, 1996), and coherence analysis to assess neural connectivity.

2. Materials and Methods

2.1. Participants

Ten healthy volunteers (7 males and 3 females, mean age: 23.4 ± 1.2 (SD)), who were identified as right handed by the Edinburgh inventory (Oldfield, 1971), participated in the present study. No participants had a history of neurological or psychological disorder, and there were no problems with vision or hearing under the present experimental conditions. Informed consent was obtained from each participant prior to the study, which was approved by the ethical committee of the Faculty of Medicine, Nagoya University.

2.2. Experimental design

The present experiment was carried out in a magnetically shielded room. Participants laid down on a bed, placing their head in the MEG dewar. A 14-inch screen was placed 30 cm in front of the participants, and a movie was projected on the screen from the outside of the room.

On the screen, an initial instruction and finger movements were presented in a movie.

Instruction for the task, observation (OB), imitation (IM) or static (ST), was first presented for 5 seconds followed by a black screen for 1 second. Then, a short movie with finger movements was projected on the screen. Finger movements consisted of five postures of fingers on a hand in one sequence: 1) a hand with two or three fingers bent, 2) all fingers bent, 3) the same finger posture as in 1), 4) all fingers bent, and 5) the same finger posture as in 1). The fingers were moved from the first to fifth postures every second in the video. In a sequence, finger postures in 1), 3), and 5) were the same, but the postures were varied in every sequence. Finger postures that had specific meanings: e.g., victory by bending the first, fourth, and fifth fingers, were not used. Each sequence of finger movements was presented from one of three perspectives: finger movements of the right hand as if his/her own hand (a first-person visual perspective, 1P-R), finger movements of the right hand of a person facing the subject (a second-person perspective, 2P-R), and finger movements of the right hand of a person in a mirror (a second-person perspective in mirror, Mirror-R) (Figs. 2 and 3). A feedback period followed for 5 seconds after the movie with finger movements. Static photos of the right opened hand from the three perspectives, 1P-R, 2P-R, and Mirror-R, were presented as the ST condition. A photo from one of three perspectives was presented for 5 seconds followed by a feedback period for 5 seconds.

For the IM task, the subjects were asked to simultaneously move their fingers similarly

to the movement in the movie. For the OB task, the subjects were asked to perform finger movements as shown in the movie during the feedback period after the movie had finished. For the IM and ST tasks, they just watched on the screen during the feedback period. For both tasks of IM and OB, the subjects were asked to show clearly their finger postures, bent or extended. An experimenter observed their finger movements from outside the magnetically shielded room through a monitor. Participants were not given any information regarding their correct or incorrect finger movements during the OB and IM tasks. When the subjects moved their fingers differently from the postures presented in a trial on the video, or they showed unclear bending or extending movements, the trial was excluded from further analysis.

Participants simply observed a static hand photo in the ST task, they had to move their fingers similarly to those presented in the movie in the IM task, and they had to memorize the finger movements presented on the movie to reproduce them after the movie in the OB task. We treated the ST condition as a basic condition without a task. Figure 3 shows the sequence of movie presentation in a task. Twelve trials of each condition were randomly repeated for each participant. Therefore, each participant performed 108 trials, 12 trials x OB/IM x 3 perspectives and 12 trials x ST x 3 perspectives, with a short rest every 10-15 trials.

2.3. MEG recording

A whole-head MEG system (PQ-1160C, Ricoh Co., Japan) with a liquid helium recycler (HCS-MEG1, FTL, Japan) was used for MEG signal recording. The MEG system had 160-channel axial-type first-order gradiometers, which were arranged in a uniformly distributed array on a helmet-type dewar, with a 50-mm-long baseline detection coil. Fiducial points for MEG were the nasion and both pre-auricular points, and the surface of the scalp of each subject was traced digitally using a 3-dimensional digitizer (SRsystem-R, Ricoh Co., Japan). Montreal Neurological Institute (MNI) stereotactic coordinates were obtained with the fiducial points and trace of the scalp surface for each subject. Pseudo-individual anatomy was created from the standard brain anatomy, the International Consortium for Brain Mapping (ICBM) 152 non-linear atlases (Fonov, Evans, McKinstry, Almlı, & Collins, 2009), using the software Brainstorm (Tadel, Baillet, Mosher, Pantazis, & Leahy, 2011). The number of vertices of the cortical surface was 15,002 in the present study on the standard brain. Further anatomical and MEG signal analyses were performed of the pseudo-individual brain. Using a pair of electrodes placed on the right hand and foot, an electrocardiogram (ECG) was recorded. Electromyogram (EMG) was also recorded from the flexor digitorum superficial muscle, using a pair of electrodes placed on the belly of the muscle and 4 cm distal, to monitor the finger movement. The MEG, ECG, and EMG signals were continuously recorded with an initial

bandpass filter of 0.3-2,000 Hz and a notch filter of 60 Hz at a sampling rate of 5,000 Hz. The MEG signals were continuously recorded during the experiment for each participant.

2.4. Data analysis

Prior to the analysis, the ECG and eye-blink artifacts were removed in the preparation process prior to analysis, using the Signal-Space Projection (SSP) and Independent Component Analysis (ICA) methods (Tesche et al., 1995; Uusitalo, & Ilmoniemi, 1997). Since we focused to investigate brain activity when a participant recognized finger movements presented from each perspective, the MEG signals for 1 second after the onset of the movie for each task were extracted at a sampling frequency of 1,000 Hz with a bandpass filter between 1 and 150 Hz.

Intra- and inter-regional functional connectivity was calculated as the synchrony of the MEG signals, which was expressed by coherence values. We obtained the coherence values using the code within Brainstorm, in which coherence analysis was based on an algorithm of minimum norm estimation (Hämäläinen, & Ilmoniemi, 1994). Coherence analysis reveals the consistency over temporal change of the phase difference between two signals as a function of the frequency, and stable phase relations receive a maximum value of 1, whereas coherence with highly random phase relations receive a score of 0 (Bardouille, & Boe, 2012).

Coherence values were calculated between two regions or in one region of interest (ROI): bilateral inferior frontal gyrus (IFG), ventral premotor area (PMv), inferior parietal lobule (IPL), superior temporal sulcus (STS), and primary sensory (S1) and motor (M1) areas, based on Destrieux's parcellation (Destrieux, Fischl, Dale, & Halgren, 2010), which were previously described as regions related to MNS (Avikainen et al., 2002; Buccino et al., 2001; Fadiga et al., 1995; Nishitani & Hari, 2000; Rizzolatti et al., 1996) (Fig. 1). The left and right sides of the regions were expressed as Rt and Lt, respectively. The software, Brainstorm, divided the cortical surface into small matrixes based on 15,002 vertices. For intra-regional coherence, each current in a matrix was estimated first and the coherence values between all combinations of two matrixes were averaged. For inter-regional connectivity, the mean current waveform in each cortical region was obtained by averaging current waveforms estimated in the small matrixes in the region. The coherence value between current waveforms in two regions was then calculated. The coherence values in each frequency range: theta between 4 and 7 Hz, alpha between 8 and 13 Hz, beta between 13 and 30 Hz, low gamma between 30 and 60 Hz, and high gamma between 60 and 90 Hz, were compared among conditions with repeated-measures two-way (tasks, perspectives) analysis of variance (ANOVA), followed by multiple comparisons with Turkey-Kramer's test. A p-value less than 0.05 was considered to be significant.

3. Results

The experiments were successfully performed by the participants. Mean incorrect trials were 1.0 (range, 0-1) and 0.5 (0-2) times in 36 OB and 36 IM trials in each subject, respectively.

Since there was no interaction indicated for any of the above combinations, the coherence values were compared among perspectives (Fig. 4) and tasks (Fig. 5). The coherence value between cortices was affected by perspectives. The values in the theta range under the 1P-R condition were higher than Mirror-R between Lt-IPL and Rt-M1 [$F(2, 54) = 3.44, p = 0.04$], and Rt-PMv and Rt-S1 [$F(2, 54) = 3.46, p = 0.04$]. In the alpha range, the coherence values on observing and imitating the 1P-R condition were higher than under the 2P-R condition. Cortical areas that showed significance were Lt-S1 and Rt-IFG [$F(2,54) = 4.18, p = 0.02$], Lt-M1 and Rt-M1 [$F(2,54) = 3.18, p = 0.05$], Lt-S1 and Rt-M1 [$F(2,54) = 4.16, p = 0.02$], and Lt-S1 and Rt-S1 [$F(2,54) = 4.23, p = 0.02$], respectively (Fig. 4). In contrast, in the low gamma range, the coherence value was higher under the 2P-R than 1P-R conditions between the Lt-IFG and Rt-M1 [$F(2, 54) = 3.42, p = 0.04$], and the Lt-M1 and Rt-S1 [$F(2, 54) = 3.17, p = 0.04$].

For intra-regional coherence, there were significant differences in values among tasks. In the theta frequency band, the coherence value of IM and OB was larger than under ST

conditions in Lt-IPL [$F(2, 67) = 59.62, p < 0.001$], Rt-PMv [$F(2, 67) = 46.11, p < 0.001$], Rt-M1 [$F(2, 67) = 61.46, p < 0.001$], and Rt-S1 [$F(2, 67) = 23.05, p < 0.001$]. In the alpha range, the coherence value was larger for IM, and OB was larger than under ST conditions in the four brain areas: Lt-S1 [$F(2,67) = 20.40, p < 0.001$], Rt-IFG [$F(2,67) = 41.99, p < 0.001$], Rt-M1 [$F(2,67) = 33.98, p < 0.001$], and Rt-S1 [$F(2,67) = 23.57, p < 0.001$] (Fig. 5). In the low-gamma band, the value was larger for IM and OB than under ST conditions in Lt-IFG [$F(2, 67) = 243.28, p < 0.001$], Lt-M1 [$F(2, 67) = 85.15, p < 0.01$], Rt-M1 [$F(2, 67) = 126.49, p < 0.001$], and Rt-S1 [$F(2, 67) = 55.18, p < 0.001$].

4. Discussion

Summarizing the results of the present study, the brain activities regarding coherence among the motor-related cortices in the frontal and central regions were modified by the visual perspectives of finger movements, and the regional activity in coherence was changed similarly in IM and OB tasks compared with the ST task.

4.1. Cerebral region modulated by visual perspectives

In the present study, we identified the effects of visual perspective on neural activity in

the brain, revealed by the difference in inter-regional coherence. The difference among visual perspectives obtained in the present study was the difference in inter-regional coherence between the first- and second-person visual perspectives.

Differences in neural activity of the brain among visual perspectives were reported in previous studies. Desynchronization of the mu rhythm in electroencephalography (EEG) was observed in the sensorimotor area (Pineda, 2005), and EEG brain activity during observing a right-handed action from an egocentric, first-person visual perspective, was greater than on observation from an allocentric, third-person visual perspective, in bilateral frontal and central regions (Drew, Quandt, & Marshall, 2015). Fu and Franz (2014) reported that mu suppression in the Rt-IFG and precentral region was specific to observation of hand movement from a first-person visual perspective, compared with a third-person visual perspective. Significant activation of the contralateral sensorimotor cortex was shown with a first-person perspective compared with third-person perspective in a previous study using fMRI (Jackson, Meltzoff, & Decety, 2006). Those previous studies suggested the involvement of sensory-motor brain regions outside visual-related cortical regions in visual perspectives. Although we observed brain activity with a different method of analysis, the present results were consistent with the previous reports, whereby information on the visual perspectives of movements facilitated sensory-motor brain regions.

We could not identify the meaning of all the changes in coherence for the cortical regions and frequencies that showed significant changes among the visual perspectives. However, the present results provide some evidence consistent with the results of previous studies. The coherence value of the alpha frequency band between the primary sensory areas in contralateral to the movement (Lt-S1) and the sensory-motor areas (Rt-IFG, Rt-S1, and R-M1) on the ipsilateral side changed with the first-person visual perspectives. The activity in the somatosensory area was responsible for translating another person's movement into one's own movement, when one observed or imitated movements performed by another person (Meltzoff et al., 1977). The brain areas showing a significant change of inter-regional coherence under the 1P-R condition included the ipsilateral S1, Rt-S1. Somatosensory activation during observation in S1 occurred ipsilaterally even more than contralaterally (Blakemore, Bristow, Bird, Frith, & Ward, 2005). It was suggested that the first-visual perspective was specifically processed in the brain, relative to the third-person perspective, in the somatosensory process. The involvement of IFG activity, as seen in the present study, for distinguishing the self from others was reported in previous studies (Jackson et al., 2006; Macuga, & Frey, 2011). As a result, in the present study, neural connection based on inter-regional coherence changed among frontal and central sites regarding the visual perspective, possibly based on the process of distinguishing self-movement from another's movement, as

suggested in a previous study (Caetano, Jousmäki, & Hari, 2007). Bilateral contributions of frontal and central regions were complex in the present study, and laterality and bi-laterality were not clear. Regions responding to visual stimuli from several perspectives were considered bilateral rather than unilateral, and, at least, brain activity for human mirror neurons for visual and motor components was not left-lateralized (Aziz-Zadeh, Koski, Zaidel, Mazziotta, & Iacoboni, 2006).

Among the PMv, IPL and STS regions, which are known as regions responsible for MNS (Agnew, Wise, & Leech, 2012), were modulated by visual perspectives in the theta band between Lt-IPL and Rt-M1 and between Rt-PMv and Rt-S1 regions. The difference was significant between the 1P-R and Mirror-R conditions. We considered that these two conditions might result in the functional difference in coherence analysis, since the Mirror-R condition provided a mirror image of the 1P-R condition.

4.2. Action observation of biological motion

In the present study, as in previous studies, the regional coherence was larger in the IM and OB tasks in the frontal and central areas than under the ST condition. The OB condition in the present study was not a simple observation but involved watching with effort to memorize the movement in order to perform it after the movie. Such observation with effort

to memorize the movement could activate similar neural processes to those activated in movement imagery, with a similar change in regional coherence to that on actual movement, at least partially in the region analyzed in the present study. Some common neural activity was observed between movement imagery and actual movement in previous studies (Stavrinou, Moraru, Cimponeriu, Della Penna, & Bezerianos, 2007; Gao, Duan, & Chen, 2011; Athanasiou, Lithari, Kalogianni, Manousos, & Panagiotis, 2012; Obayashi, Uemura, & Hoshiyama, 2017). We considered that the observation of movement might induce neural processes in the sensory-motor and movement-related cortical areas similar to those on actual movement.

For MNS-related brain regions, there was a significant difference in intra-regional coherence in the theta frequency band in Lt-IPL and Rt-PMv. Those regions were also modified in inter-cortical coherence among visual perspectives, as described above. Although we could not extract a modification of coherence as a specific function of MNS, the present results suggest that both neural networks for MNS and the sensorimotor system were facilitated by a combination of visual information on perspectives and motor tasks.

Regarding inter- and intra-regional coherence, the results should be interpreted with caution. During sensorimotor tasks, event-related desynchronization (ERD) has been reported (Pineda, 2005), as well as tasks related to MNS (Yin, Liu, & Ding, 2016). We revealed

that brain regions showing significant changes in coherence among conditions were responsible for the condition of performance, but we could not clarify the detailed significance of the findings regarding neural mechanisms, e.g., how the high/low value in coherence and regional ERD corresponded with each other, and what they meant in the neural network.

In the present study, we investigated brain activity on the observation of one hand, the right hand, from different perspectives. The Mirror-R condition in the present study was identical to the 2P-L, left hand of a second person, condition. Brain activity for mirror image and counter-balance of the dominant/non-dominant hand could be different or overlap, depending on the cognitive strategy of the participants. The relationship between a mirror image and counter-balance should be considered and analyzed in future studies.

4.3. Relationship with clinical practice

The results of the present study suggest that the action observation from different perspectives was processed differently in the brain. Action observation has generally been used in action or movement learning in rehabilitation for patients with various motor disturbances, as well as training in sports. Different brain activity when observing from different perspectives suggests that a specific brain lesion or pathology could cause selective or relative difficulty viewing from a certain perspective. In intervention and training by

showing body movements, it might be necessary to consider the observer's visual perspective.

4.4. Limitations and further studies

The present study analyzed the difference in neural mechanisms regarding visual perspectives. As described above, we could not refer to the neural mechanism based on the results of inter- and intra-regional coherence analysis, but could identify responsible regions based on the visual perspectives of motion. Neural connectivity revealed by coherence analysis among selected regions might be modulated by neurons outside the regions. Analysis of neural activity in the candidate regions with various patterns of stimuli would provide further information. The contribution of the IPL (Buccino et al., 2001) and PMv (van Elk, 2014) areas to movement observation, and M1 to the matching system mapping on observed action onto one's own body and motor representations (Buccino et al., 2001) were reported. These candidate areas may be involved in any movement, and we could not clarify mechanisms in these areas specific to the present experiment. In addition, the PMv, IPL, and STS regions, which are known as regions responsible for MNS (Agnew et al., 2012), were not modulated by visual perspectives in the present study. Since all visual stimuli used in the present study, including the ST task, were figures of another's body, the MNS may have been involved in every stimulation to some extent in the present study.

The present experiment was solely conducted with participants in a prone position due to the restriction of the MEG system. The relationship between perspectives of body action and a participant's position, e.g., sitting or standing, should be studied in further studies.

Inter-individual differences in coherence values, as expressed by standard deviations in Figs. 4 and 5, were large in some conditions or brain regions, although the pattern of change was similar. Inter-individual variation in the coherence value might be due to differences in brain activity related to each participant's effort or strategy during the task; however, we could not reach any conclusion regarding this phenomenon.

5. Conclusion

The present study was aimed to investigate the effects of visual perspectives on neural connectivity among motor- and MNS-related cortical regions. The brain activity in coherence was modified among frontal, central, sensorimotor, and MNS-related regions by the visual perspectives on finger movements. The regional activity in coherence was changed similarly in the IM and OB tasks compared with the ST task. Both neural networks for MNS and the sensorimotor system were facilitated by a combination of visual information on perspectives and motor tasks.

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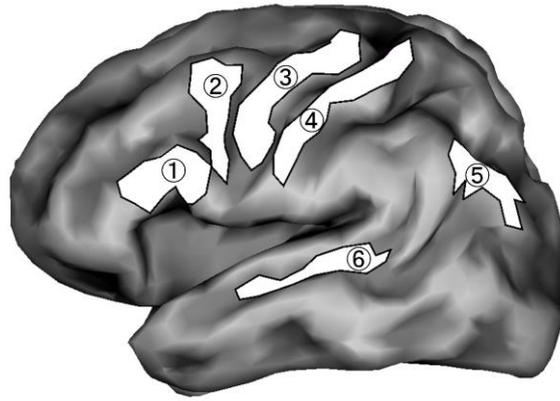


Figure 1: Regions of interest for coherence analysis. Six cortical areas were selected in each hemisphere: ① inferior frontal gyrus, ② ventral premotor area, ③ primary motor area, ④ primary sensory area, ⑤ inferior parietal lobule, ⑥ superior temporal sulcus.

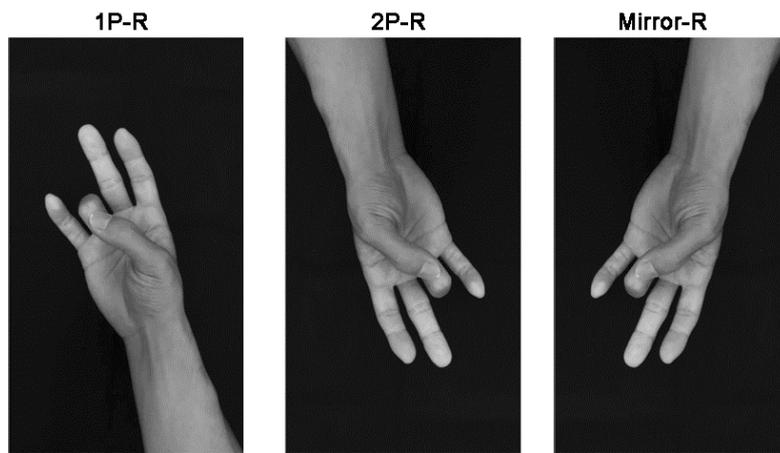


Figure 2: Three perspectives on right finger movements. Left: first-person visual perspective (1P-R), middle: second-person visual perspective (2P-R), and right: the right hand on a mirror (Mirror-R).

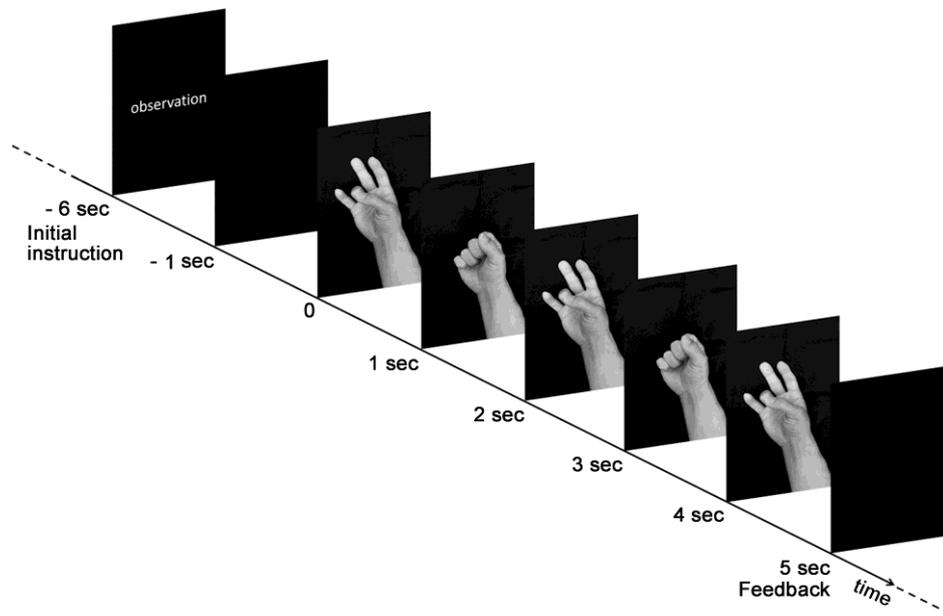


Figure 3: Visual presentation for the experiment during the observation (OB) or imitation (IM) task. Visual presentation for a trial comprised of an initial instruction period, from -6 to -1 sec, finger movement, from 0 to 5 sec, and a feedback period for the OB task, after 5 sec. Instruction for the task, observation, or imitation was first presented for 5 seconds followed by a black screen for 1 second. Then, a short movie with five finger movements was projected on the screen (see text). During the feedback period, participants moved their fingers as shown on the movie for the OB, or they just watched on the screen for the IM task.

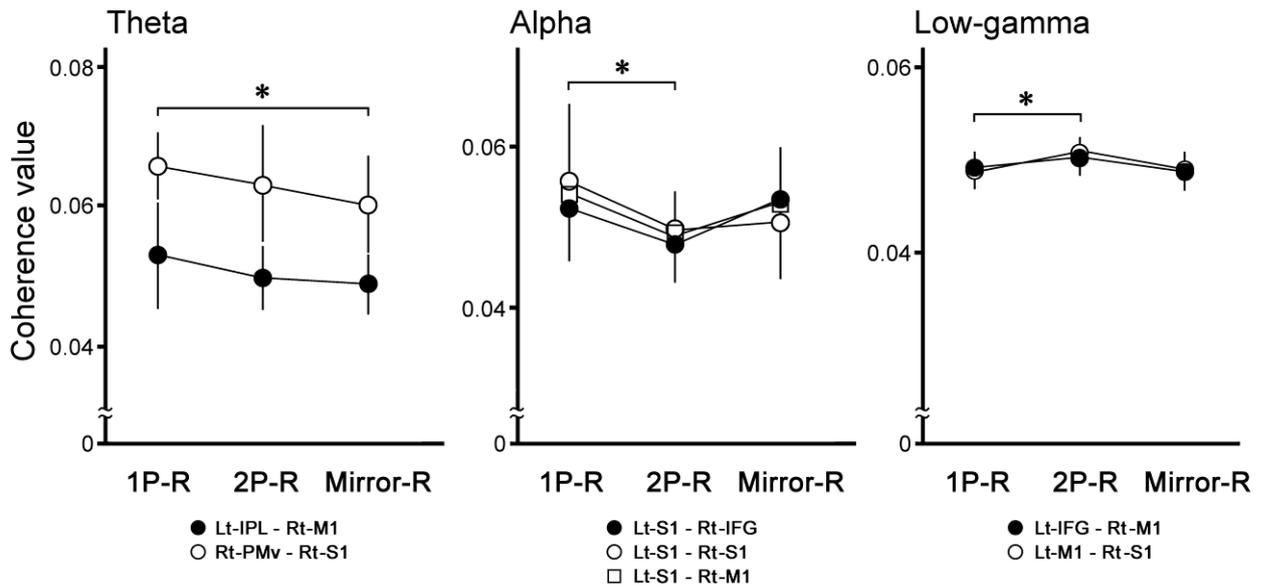


Figure 4: Left: coherence of the theta frequency band, 4-8 Hz, was larger with the first-person visual perspective (1P-R) than for the right finger movements on a mirror (Mirror-R) between the left inferior parietal lobule (Lt-IPL) and right primary motor area (Rt-M1), and between the right ventral premotor area (Rt-PMv) and right primary sensory area (Rt-S1). Middle: coherence of the alpha frequency band, 8-13 Hz, was larger for 1P-R than 2P-R between the left S1 (Lt-S1) and right inferior frontal gyrus (Rt-IFG), between Lt-S1 and Rt-M1, and between Lt-S1 and Rt-S1. Right: coherence of the low-gamma band, 30-60 Hz, was larger for 2P-R than 1P-R between the left IFG (Lt-IFG) and Rt-M1, and between the left M1 (Lt-M1) and Rt-S1. * $p < 0.05$, Turkey-Kramer's test. Each vertical bar indicates a standard deviation (SD) among participants.

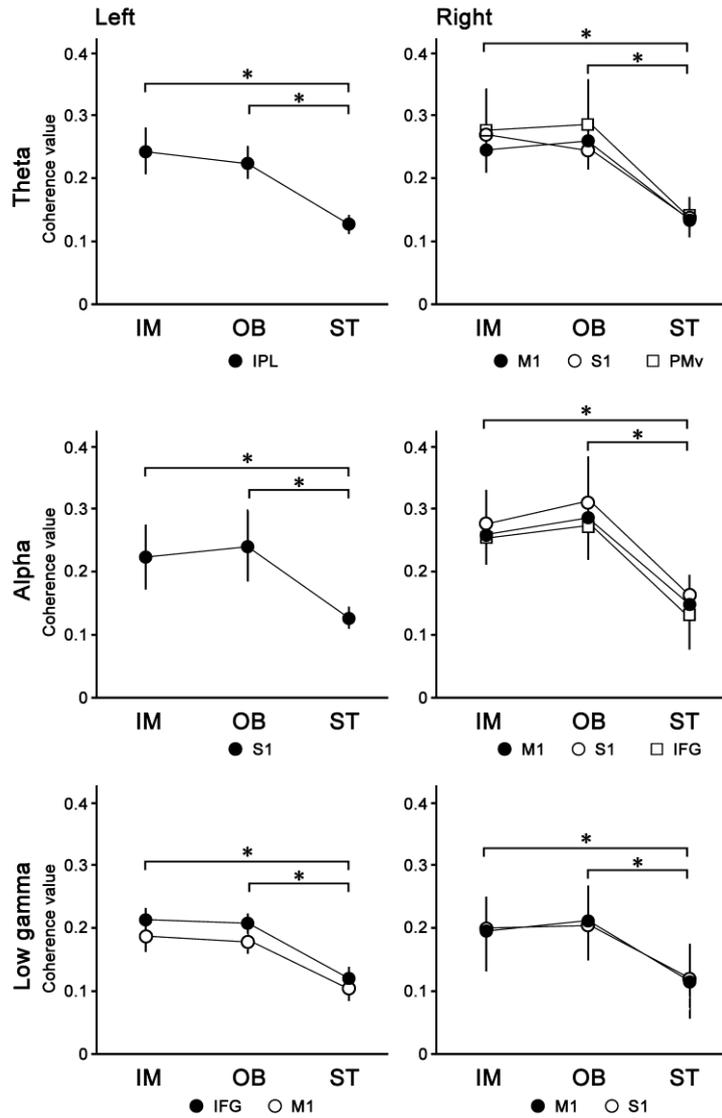


Figure 5: Intra-regional coherence among conditions. Upper: theta frequency band, the coherence value of imitation (IM) and observation (OB) was larger than under static (ST) conditions in the left inferior parietal lobule (IPL), right ventral premotor area (PMv), right primary motor area (M1), and right primary sensory area (S1). Middle: alpha frequency band, the coherence value of IM and OB was larger than under ST conditions in four brain areas: left S1, right inferior frontal gyrus (IFG), right M1, and right S1. In the low-gamma band, the value was larger in IM and OB than under ST conditions in the left IFG, left M1, right M1, and right S1. * $p < 0.01$, Tukey-Kramer test. Each vertical bar indicates a standard deviation (SD) among participants.