

Investigation of a flexible inhibitory process of automatic imitation and its individual differences: An EEG study

西村, 悠貴

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PhD thesis

Investigation of a Flexible Inhibitory Process of
Automatic Imitation and its Individual Differences:
an EEG Study

Yuki Nishimura

Graduate School of Integrated Frontier Sciences

Kyushu University

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Chapter 1 Introduction

1.1 The social brain

Throughout human evolution, cooperation and society forming have always increased the species' chances for survival. It has been suggested that humans as social animals possess advanced social cognitive abilities compared with other creatures on the planet (Gazzaniga, 2008). Society is formed through various interactions, because the formation of a society requires the presence of others. The human social brain, consisting of multiple brain regions, is responsible for the information processing necessary to facilitate these interactions (Dunbar & Shultz, 2007). Self-recognition and discrimination from others are among the most important functions in these interactions. A number of studies have reported that the prefrontal cortex is responsible for such kinds of processing (Ochsner et al., 2005). The volume ratio of prefrontal cortex relative to the entire brain is thought to reflect the degree of socialization. It is only 3.5% in cats; however, it goes up to 11.5% in monkeys, 17% in chimpanzees, and 29% in humans (Fuster, 1997). Moreover, the volume ratio of the frontal part is known to correlate with the size of the society that each species forms (Hill & Dunbar, 2003). While this evidence indicates that there is an evolutionary aspect of the social brain, a developmental aspect has also been found. For example, the lower order ability of Theory of Mind (ToM) emerges around four years after birth, and higher order ability is formed around nine years old (Wellman, Cross, & Watson, 2001). Self-recognition is essential to pass a ToM task, and it is highly dependent on the functional maturation of prefrontal cortex known to occur around the same period of our development (Ritblatt, 2000).

As discussed above, social interaction requires efficient processing of information of the self and others. To meet that demand, some brain activities, such as automatic imitation, do not distinguish the self from others, whereas others do. Not only one, but both types of brain activity are essential for smooth interaction. In the present study, focusing on

automatic imitation and its flexible modulation, I examined the processing of physical information handled by the social brain.

1.2 Automatic imitation and its physiological measures

Imitation, which is a reproduction of observed action by the observer, is one of the major psychological functions supporting not only social interaction, but also social cognition (de Waal, 2012; Decety & Svetlova, 2012). In addition to physical imitation, in-brain automatic imitation is one of the core functions underlying abilities of social cognition such as empathy (Carr, Iacoboni, Dubeau, Mazziotta, & Lenzi, 2003; Ferrari, Gallese, Rizzolatti, & Fogassi, 2003; Gallese, 1998; Molenberghs, Cunnington, & Mattingley, 2009; Rizzolatti & Sinigaglia, 2010; Woodruff, Martin, & Bilyk, 2011). The suggested underlying neural mechanism of imitation is a brain system called the human mirror neuron system (hMNS) (Iacoboni et al., 1999; Rizzolatti & Craighero, 2004) in the action observation network (AON) of the human brain (E. S. Cross, Hamilton, Kraemer, Kelley, & Grafton, 2009; Iacoboni & Mazziotta, 2007; Rizzolatti & Craighero, 2004). This network is thought to operate various functions, such as action understanding and prediction (Kilner, Friston, & Frith, 2007; Rizzolatti, Fogassi, & Gallese, 2001; Schütz-Bosbach & Prinz, 2007), inferring the intention of others (Fogassi et al., 2005; A. F. d. C. Hamilton & Grafton, 2006; Kilner, Marchant, & Frith, 2006), and social cognition (Iacoboni & Dapretto, 2006). In addition, it is perhaps related to motor control and motor planning (Brown, Martinez, & Parsons, 2006; Caroline Catmur, Walsh, & Heyes, 2007; Grafton & de C. Hamilton, 2007; Williams, Whiten, Waiter, Pechey, & Perrett, 2007). Thus, hMNS is responsible for replicating the motor representation of an observed action as one component of the variety of functions of the AON.

The human mirror neuron system is a cluster of mirror neurons activated during both the performance and observation of body movements (Iacoboni, 2009). The neurons were named after their mirroring characteristics by Rizzolatti and his colleagues, who first discovered the neurons during an experiment on the motor neurons of macaque monkeys (di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; Gallese, Fadiga,

Fogassi, & Rizzolatti, 1996; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996). The cluster of putative mirror neurons in the human brain is the hMNS, and is thought to constitute a brain system that behaves similarly to the mirror neurons found in monkeys. The existence of a mirror neuron system in the human brain was suggested by studies using neurophysiological techniques to measure human brain activity such as positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) (Babiloni et al., 2016; Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995; Fox et al., 2016; Hobson & Bishop, 2016; Strafella & Paus, 2000). In addition to evidence from non-invasive methods, mirror-like brain activity measured through single-cell recording also supports the existence of a mirror neuron system in human brain based on recordings of action potentials during both the execution and observation of actions (Mukamel, Ekstrom, Kaplan, Iacoboni, & Fried, 2010); however, the number of studies employing single-cell recording is very low for ethical reasons.

Functional magnetic resonance imaging, PET, magnetoencephalography, motor-evoked potentials (MEP), and electroencephalograms (EEG) have been used to assess hMNS activity in humans because invasive techniques cannot be used. The sensory-motor mu wave is the most widely used index in the assessment of hMNS activity using EEG. Similar to hMNS activity, mu wave power is suppressed by both the execution and observation of actions (Bowman et al., 2017; Braadbaart, Williams, & Waiter, 2013; Hobson & Bishop, 2016; Perry & Bentin, 2010; Takemi, Masakado, Liu, & Ushiba, 2013). Moreover, it is known that hand movements have a pronounced effect on brain responses, as measured by mu suppression (Isoda et al., 2016; Perry & Bentin, 2010). Due to its ease of application (even for small children), relatively high temporal resolution, and low economic burden, treating the EEG mu wave as an hMNS activity index has expanded the opportunities to study it; for example, studies with child participants across age groups have become very easy to conduct (Nishimura, Ikeda, Suematsu, & Higuchi, 2018). Mu wave event-related desynchronization (mu ERD) can

be calculated as the hMNS activity index when the stimuli are repeatedly presented. The amount of mu wave power suppression relative to the baseline period, which are inserted just before each stimulus onset, are shown in dB or %. Negative value in ERD is interpreted as stronger cortical excitability. Validation studies of mu suppression as a measure of hMNS activity performed by spontaneously recording of fMRI and EEG have shown that mu wave reduction is a reliable measure of hMNS activity. On the other hand, in these studies, it has also been indicated that mu wave suppression is easily contaminated by the occipital alpha wave, which has larger power than the mu wave and may also reflect the activity of brain regions not associated with hMNS (Braadbaart et al., 2013; Fox et al., 2016; Hobson & Bishop, 2016). Therefore, although it is a useful measure of hMNS activity due to its characteristics, the index must be interpreted with caution to ensure data quality. There are several ways to do so, such as measuring baseline power frequently, including the occipital alpha in the region of interest, and applying technologies to estimate the sources of brain activity.

1.3 Inhibition of automatic imitation

Although automatic imitation supported by the hMNS in the AON is a core brain function for social interaction and cognition, imitation is obviously not always the most appropriate reaction in daily situations. Moreover, in some cases, mirroring may be even counterproductive (Brass, Bekkering, Wohlschläger, & Prinz, 2000; Brass, Zysset, & von Cramon, 2001). Therefore, inhibition of imitative behavior and in-brain imitation is very important to facilitate smooth complementary and joint actions (Campbell & Cunnington, 2017; Cross & Iacoboni, 2014b; Cross, Torrisi, Reynolds Losin, & Iacoboni, 2013). For example, when taking a cup or glass from another person, the receiver should inhibit his or her imitative motor action in favor of an appropriate response in order to avoid taking the same part of the object by which the sender is holding the cup or glass, which would destabilize the object (Newman-Norlund, van Schie, van Zuijlen, & Bekkering, 2007; Ocampo, Kritikos, & Cunnington, 2011). Given the existence of imitative congruency, a discordance between the observed and intended actions and an increased workload in information processing is observed in prolonged reaction time and increased brain activity (Brass et al., 2000, 2001; Cross & Iacoboni, 2014b). It has also been found that hMNS activity is modulated by social attitude (Cook & Bird, 2011; Leighton, Bird, Orsini, & Heyes, 2010) and social relevance (Kilner et al., 2006). According to Kilner et al., modulation is thought to reflect a mechanism that allows only socially relevant information to be passed to the hMNS and filters out others.

Initially, difficulties in social cognition as a characteristic of autism spectrum disorder (ASD) were understood as a result of the decreased functionality of hMNS (Bernier, Aaronson, & Kresse, 2014; Cossu et al., 2012; Kim et al., 2015; Oberman et al., 2005, 2013; Oberman, Ramachandran, & Pineda, 2008; Pierre L., 2015; Rizzolatti & Fabbri-Destro, 2010; Rizzolatti, Fabbri-destro, & Cattaneo, 2009; Théoret et al., 2005). However, such a “broken mirror” hypothesis has been questioned recently from various

perspectives. Such characteristics cannot originate within a single brain system but must rather be due to the malfunction and miscoordination of multiple brain systems (A. F. de C. Hamilton, Brindley, & Frith, 2007; Williams et al., 2006). Moreover, the decreased functionality of frontal brain regions modulating hMNS activity and the self-other distinction is currently thought to be related to decreased social cognitive abilities in ASD patients (Southgate & de C. Hamilton, 2008; Spengler, Bird, & Brass, 2010). Thus, the importance of the flexible control of automatic imitation is also suggested by studies of autistic symptoms.

There is ongoing debate over which brain network is responsible for controlling automatic imitation. Initially, “social brain” regions related to the ToM were found to be active during an imitation-inhibition task, indicating that the inhibitory system of imitative response tendencies consists of several brain regions, including the temporoparietal junction, dorsolateral prefrontal cortex, right frontopolar cortex, right anterior parietal cortex, and precuneus (Amodio & Frith, 2006; Brass et al., 2001; Saxe & Kanwisher, 2003; Van Overwalle, 2009). In addition, an imitation-inhibition task applied as training for social cognitive skills was found to be effective in improving participants’ abilities in social perspective taking, even one day after the training session (Santesteban et al., 2012). This is a further evidence for the involvement of the ToM network in modulating imitative response. Accordingly, a theory that key brain systems for social interaction also regulate imitative brain responses was proposed (Brass, Ruby, & Spengler, 2009).

However, a domain-general brain network related to broad types of reaction-inhibition has more recently been implicated in imitation-inhibition as well (Bien, Roebroek, Goebel, & Sack, 2009; Cross & Iacoboni, 2013; Darda, Butler, & Ramsey, 2018; Marsh, Bird, & Catmur, 2016). This suggested brain network is called the multiple demand (MD) network because of its engagement in a wide range of mental processing

(Duncan, 2010). The network has been localized in the dorsal frontoparietal cortices, supplementary motor area, and anterior insula by a number of studies (Aron, Robbins, & Poldrack, 2014; Bunge, Hazeltine, Scanlon, Rosen, & Gabrieli, 2002; Hazeltine, Poldrack, & Gabrieli, 2000; Nee, Wager, & Jonides, 2007; Wager et al., 2005). Moreover, as numerous studies have reported the participation of both domain-general and domain-specific networks, the inhibition of automatic imitation may be realized by the complex cooperation of higher-order cognitive functions.

While most of the studies have focused on the brain networks responsible for the “modulating” side of automatic imitation, little attention has been paid to the “modulated” automatic imitation using physiological measures. Besides, behavioral measures such as reaction time and the proportion of correct responses have been used widely to evaluate the effect of the “modulation” originating from imitative congruency. One study employed MEP to measure the preparatory control of automatic imitation (Cross & Iacoboni, 2014b). In that study, hMNS activity was measured during an action observation period inserted before the target video that required participants to respond. Three experimental conditions were compared: 1) imitation with preparation, 2) counter-imitation with preparation, and 3) no prior information (imitation or counter-imitation). It was found that hMNS activity was suppressed under Conditions 2 and 3 but not under Condition 1. Another study that employed MEP indicated that hMNS activity during action observation can be eliminated by prior instructions (Bardi, Bundt, Notebaert, & Brass, 2015). The authors claimed that mirror representations created by mirroring brain activity are overwritten by the stimulus-response association activated by the instruction in order to achieve a flexible adjustment of mirror responses in a variety of contexts. These studies highlighted the inhibition of automatic imitation by physiological measures; however, data acquired during the actual response are still lacking.

The number of studies examining the relationship between the “modulating” and the “modulated” brain activities simultaneously is even lower. A study by Cross et al. employed a dynamic causal modeling (DCM) technique with fMRI scans to address the relationship between the inhibiting process and the inhibited process for automatic imitation (Cross et al., 2013). Their winning model as determined by DCM comprised a network consisting of the anterior cingulate cortex (ACC), medial prefrontal cortex, and anterior insula as the “modulating” network and the inferior frontal gyrus pars opercularis (IFGpo) as the “modulated” hMNS network. As a result, there was a trend of functional connectivity found between anterior insula and IFGpo ($p = .07$). Therefore, further research investigating the link between automatic imitation and the brain activity modulating it is warranted.

1.4 The proposed task to investigate the inhibition of imitation

The imitation-inhibition task is designed to evaluate the level of inhibition of imitative tendencies using reaction time as a prior index (Brass et al., 2009, 2001). The task has been adopted in a number of studies to test the conditional or individual ability to inhibit imitative response tendencies (Brass et al., 2000, 2009, 2001; Campbell, Mehrkanoon, & Cunnington, 2018; Cross & Iacoboni, 2014b; Darda et al., 2018; Sowden & Catmur, 2015; Watanabe, Higuchi, & Kikuchi, 2013). In the task, participants are required to respond by lifting either their index or middle finger as soon as possible while observing congruent (facilitating) or incongruent (interrupting) finger movements presented simultaneously with the action cue. The congruency effect on task execution is measured by comparing the indices of congruent and incongruent trials. The effect of imitative congruency is often measured by subtracting the data from congruent trials from the data from incongruent trials (e.g., Δ RT [reaction time]). It is important to dissociate spatial compatibility effects from those of imitative compatibility effects when investigating the brain processes of imitation-inhibition (Darda et al., 2018). Generally, this is accounted for by adding a condition showing similar movement without biological motion in the stimuli.

In the major versions of the tasks, the finger to lift is indicated by a non-biological symbol such as a numerical character, or it is designated before the experiment and participants have to respond regardless to the stimuli. Thus, finger stimuli are regarded as distractors and participants are expected to ignore them when the incongruent response is required. However, because ignoring an observed action and making a response based on non-biological information is not a good simulation of daily life, this version of the task focuses on particular kinds of daily situations. A version that tells the required type of response (congruent or incongruent) beforehand also has the problem of alignment with daily situations. Various modifications have been made in various studies, yielding a variety of versions of the task. Notably, Cross and Iacoboni used a

colored frame in a video that depicted fingers being lifted to instruct participants on whether to respond with the finger congruent or incongruent to the finger lifted on the screen in order to investigate the preparatory inhibition of motor resonance through changing the timing of the presentation of the colored frame (Cross & Iacoboni, 2014a). In this version of the task, the video cannot be ignored but provides important information on which finger to respond with even in the incongruent trials. Thus, it can be said that Cross and Iacoboni's is more likely to replicate situations of daily life in which the action itself contains important information.

1.5 Using EEGs to measure inhibition of imitation

Functional magnetic resonance imaging is the most widely used technique to assess brain activity during an imitation-inhibition task. However, electrophysiological techniques are less used in this field of study. Although the spatial resolution of EEG is very low, by using it to measure brain activity related to the inhibition of imitating behavior, we may conduct experiments relatively easily and with higher temporal resolution than fMRI. Magnetoencephalography has not only high temporal resolution, but also high spatial resolution; however, its cost is much higher than that of EEG. High temporal resolution is useful especially when one would like to focus on sudden flexible decision-making and response execution in comparison with preparatory behavior control. In other words, when participants are required to respond without information on the required type of response (e.g., congruent or incongruent), the temporal resolution of fMRI may not be sufficient to trace the time courses of brain activities occurring according to task demands.

A recent study used the event-related potentials (ERPs) of EEG to assess brain activity while participants coped with an imitation-inhibition task (Deschrijver, Wiersema, & Brass, 2017). In that study, the authors focused on the stimulus-locked N190, readiness potential, and central P3 component as indices of the visual processing of body parts (Thierry et al., 2006), motor preparation (Leuthold & Schröter, 2011), and self- versus other-related processes in the paradigm of social cognition (Knyazev, 2013; Kühn et al., 2011; Sebanz, Knoblich, Prinz, & Wascher, 2006), respectively. The incongruent trials showed greater N190 amplitude and smaller central P3 amplitude, suggesting an increased visual processing load and self-other distinction originating from imitative congruency. In addition, congruency effects on reaction time and central P3 amplitude showed a significant positive correlation. On the other hand, in this study, effect of spatial compatibility was accounted too low and the brain activity for the automatic imitation was not itself assessed by the physiological measures. There are other studies

that have used EEG; however, they mainly focused on action planning or emotion perception (Grecucci, Balaban, Buiatti, Budai, & Rumiati, 2009; Sebanz et al., 2006).

Event-related potential is one of the most widely used EEG indices in cognitive psychology and psychophysiology. In particular, the N2 and P3 components of ERP are the best-known components observed during tasks that require response selection and inhibition (Donkers & van Boxtel, 2004; Kopp, Mattler, Goertz, & Rist, 1996; Smith, Johnstone, & Barry, 2008). The N2 component is a negative peak observed about 200–400 ms after stimulus onset in the frontal region on the scalp. It reportedly reflects conflict monitoring and struggles to decide between options, which is a non-motoric stage of inhibition (Donkers & van Boxtel, 2004; Nieuwenhuis, Yeung, van den Wildenberg, & Ridderinkhof, 2003). Meanwhile, the P3 component is a positive peak observed around 400–600 ms after stimulus onset. It is known to reflect motor inhibition (Smith et al., 2008). The ACC is reported to be responsible for both domain-general motor inhibition (Botvinick, Nystrom, Fissell, Carter, & Cohen, 1999) and the inhibition of automatic imitation (Amodio & Frith, 2006; Cross et al., 2013). Importantly, a source analysis of the N2 component observed in a cued go/no-go task indicates the medial frontal regions, including the ACC, as its source (Bekker, Kenemans, & Verbaten, 2005).

1.6 Individual differences in social cognitive traits

Though humans possess highly sophisticated social cognitive abilities, individual differences exist with regard to social cognitive traits. The ability to flexibly suppress automatic imitation also differs among individuals, possibly by several factors (Brass et al., 2000; Butler, Ward, & Ramsey, 2015; de Guzman, Bird, Banissy, & Catmur, 2016).

Among the theoretical approaches, there has been an attempt to quantify human personality based on causal cognition. Baron-Cohen developed the empathizing-systemizing model and EQ/SQ questionnaire to explain individual cognitive traits in terms of two psychological “drives” (Baron-Cohen, 2002). Empathizing is a drive that identifies another’s emotions or thoughts and leads an individual to react with an appropriate emotion by analyzing psychological causal relations. By contrast, systemizing is a drive that analyzes factors of systems and derives basic patterns that defy the function of the system. The term “system” here covers all processes, from physical law to social phenomena, that have any kind of law-like nature (Baron-Cohen, 2002; Wakabayashi, Baron-Cohen, & Wheelwright, 2006).

Although variation among individuals exists in imitation-inhibition performance and EQ/SQ scores, no study has aimed to address the relationship between an individual’s cognitive style and performance on flexible inhibition of imitation.

1.7 Aim of the present study

This study aimed to use EEG to investigate the participation of the frontal brain networks, such as the MD network, in the flexible inhibition of imitative responses by adopting the widely-used ERP paradigm and its indices of response inhibition to study automatic imitation. While investigating the inhibition of automatic imitation by the frontal brain network, I especially focused on the sudden flexible control of hMNS compared with the preparatory control of automatic imitation. In addition, individual differences in inhibiting brain activity were also investigated using a questionnaire to assess individual social cognitive traits and correlation analysis.

1.8 Structure of the thesis

This thesis consists of five chapters. In the first chapter, I discussed the background of the research, such as automatic imitation and its inhibition, and indicated the aim of the research. In Chapter 2 and Chapter 3, two similar experiments with slight differences in task settings are reported. By conducting two experiments, I aimed to test the usability of ERP components as indices of imitation-inhibition first and investigate the relationship between frontal brain activity and hMNS activity using correlation analysis. In Chapter 4, the individual differences in hMNS activity during an imitation-inhibition task are analyzed using a self-assessment questionnaire that measures empathy and systemizing quotients. Finally, in Chapter 5, I provide a conclusion concerning all the experiments, discuss their limitations, and indicate some possible approaches for future research.

The content of Chapter 4 has been published as a research article, entitled “The Relationship Between Inhibition of Automatic Imitation and Personal Cognitive Styles,” in the *Journal of Physiological Anthropology* (Nishimura, Ikeda, & Higuchi, 2018).

Chapter 2 Investigating the flexible inhibitory control of automatic imitation using EEG (Experiment 1)

2.1 Introduction

In previous studies investigating the putative modulation of hMNS activity by the frontal brain regions, fMRI is the technique that has been employed most. However, very little experimental work using EEG has been conducted on the effect of imitative congruency (see Section 1.5). If EEG is found useful for measuring inhibitory brain activity, its relatively high temporal resolution and economic benefits will afford us deeper insights into the field of study.

As introduced in Chapter 1.4, there are variety of modifications that have been made to the original imitation-inhibition task. The majority of earlier studies presented finger movement as a distractor to be ignored. On the other hand, in daily situations, the actions of others cannot be ignored. Therefore, in the current experiment, the presented finger movement was not only used as a distractor but also as a task indicator.

Participants were required to make a decision based on the finger movement (index or middle finger lifting) and colored frame as a task indicator (congruent or incongruent response required) presented simultaneously. This version of the task was initially proposed by Cross and Iacoboni to assess a preparatory control of imitative tendencies (Cross & Iacoboni, 2014b).

In the current experiment, as a first step to assess brain activities by EEG, I aimed to investigate whether the selected EEG indices reflect the brain activity elicited by the task. I interpreted the congruent trial as the standard trial (natural state=automatic imitation) and the incongruent trial as the target trial that requires inhibition and measured ERPs during the task. Because the involvement of the domain-general MD network for response inhibition has been repeatedly reported even in the inhibition of imitation (Bien et al., 2009; Cross et al., 2013; Darda et al., 2018; Marsh et al., 2016), I expected to observe a similar form of ERPs elicited by the imitation-inhibition task to those observed in previous go/no-go or go/go tasks. In order to assess the activity of

“modulated” automatic imitation by EEG, I calculated the ERD of the sensory motor mu rhythm from exactly the same EEG data as the ERPs.

I hypothesized that if frontal activity is responsible for the flexible modulation of automatic imitation: 1) the congruency effect will be observed in both ERPs and ERD, and 2) the congruency effect on the ERPs will be correlated with the effect on the ERD because the DCM analysis revealed a possible functional link between the frontal and hMNS network (Cross et al., 2013). In order to avoid the effects of different numbers of congruent and incongruent trials, the ratio of trials was set at 50:50. However, in such an experimental setting, the effect of imitative congruency may be hard to observe because the N2 and P3 amplitudes are known to show small or no difference between go and no-go trials (Bekker et al., 2005). In addition, as another concern, if the probability of congruent and incongruent trials are the same, participants may prepare their reactions for the more difficult incongruent trials. To address these points, Experiment 2 was conducted separately and discussed in the next chapter.

2.2 Methods

2.2.1 Participants

Twenty-seven young adults participated in the study (12 females and 15 males, 23.30 ± 1.27 years old). The Edinburgh Handedness Inventory confirmed that all participants were right-hand dominant. Participants were naive as to the purpose of the experiment and were informed before the study that their privacy would be secure. All participants provided written informed consent prior to starting the experiment, and they were debriefed following the completion of the experiment. The procedure of the study was approved by the Ethics Committee of Kyushu University. The study was conducted according to the principles of the Declaration of Helsinki.

2.2.2 The imitation-inhibition task

A similar version of the imitation-inhibition task used in the earlier study (Cross & Iacoboni, 2014b) was employed. Participants were required to respond by lifting their index or middle finger as soon as possible according to the simultaneously presented finger movement and indicator of the required response (congruent or incongruent). In order to take spatial compatibility effect into account, in addition to the described imitation condition, a spatial condition, in which one of two black dots moved upward instead of fingers, was also conducted. The order of the conditions was counterbalanced across participants.

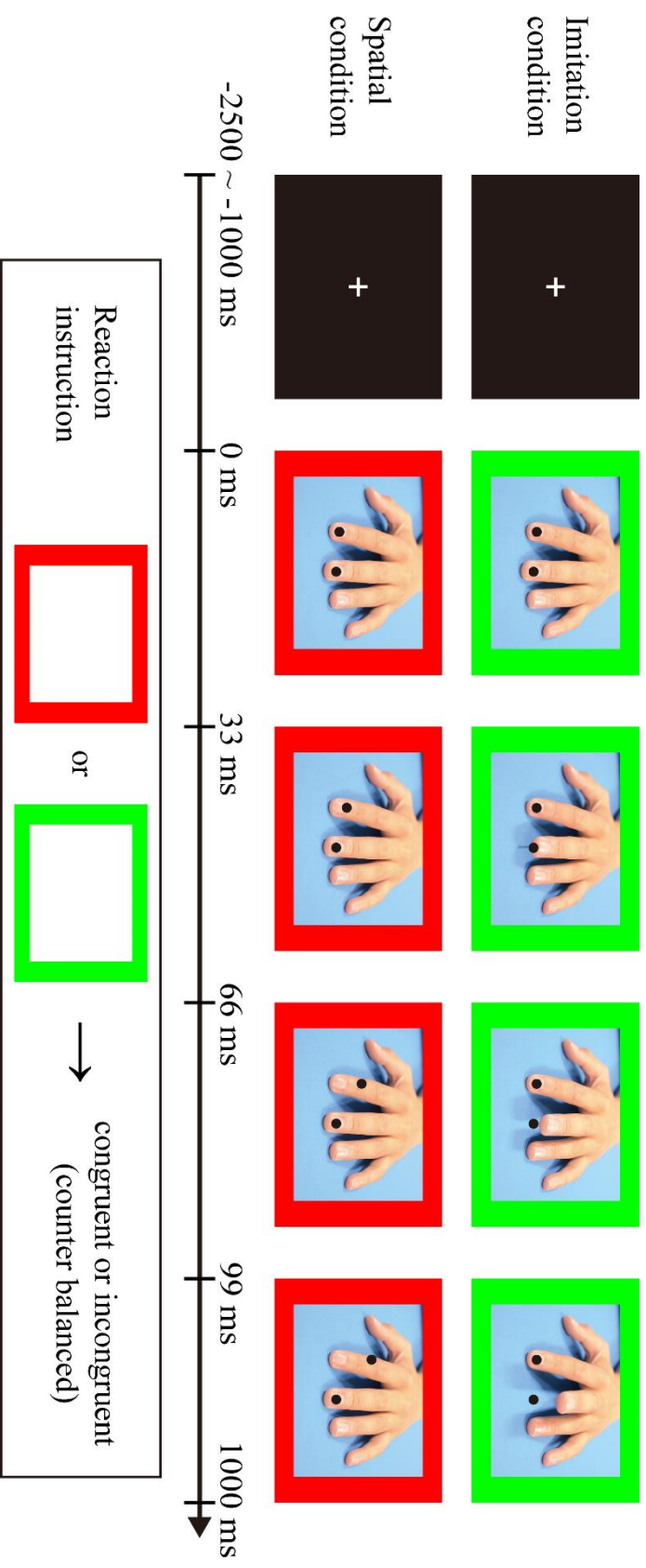


Figure 1 Example of the stimuli used in the experiment. After the inter-stimulus interval of 1000–2500 ms, a video depicting a finger being lifted in four frames was presented subsequently. The simultaneously presented colored frame indicates either congruent or incongruent finger lifting by the participants. The onsets of each frame are given in milliseconds.

Equal numbers of congruent and incongruent trials were presented in random order in both conditions (a total of 300 trials; 150 trials each for congruent and incongruent trials). After every 100 trials, short breaks were inserted to maintain the participants' focus.

The video presented showed a hand quickly lifting an index or middle finger in a surrounding colored frame (red or green). The frame's color indicated whether the reaction should be made with the congruent or incongruent finger (Figure 1). For example, if the red frame is assigned to the incongruent response, lifting the middle finger is a correct response in both conditions illustrated in the figure. In the spatial condition, black dots instead of fingers moved upward with the same velocity as the finger stimuli. The correspondence of color and instruction was counter-balanced across participants.

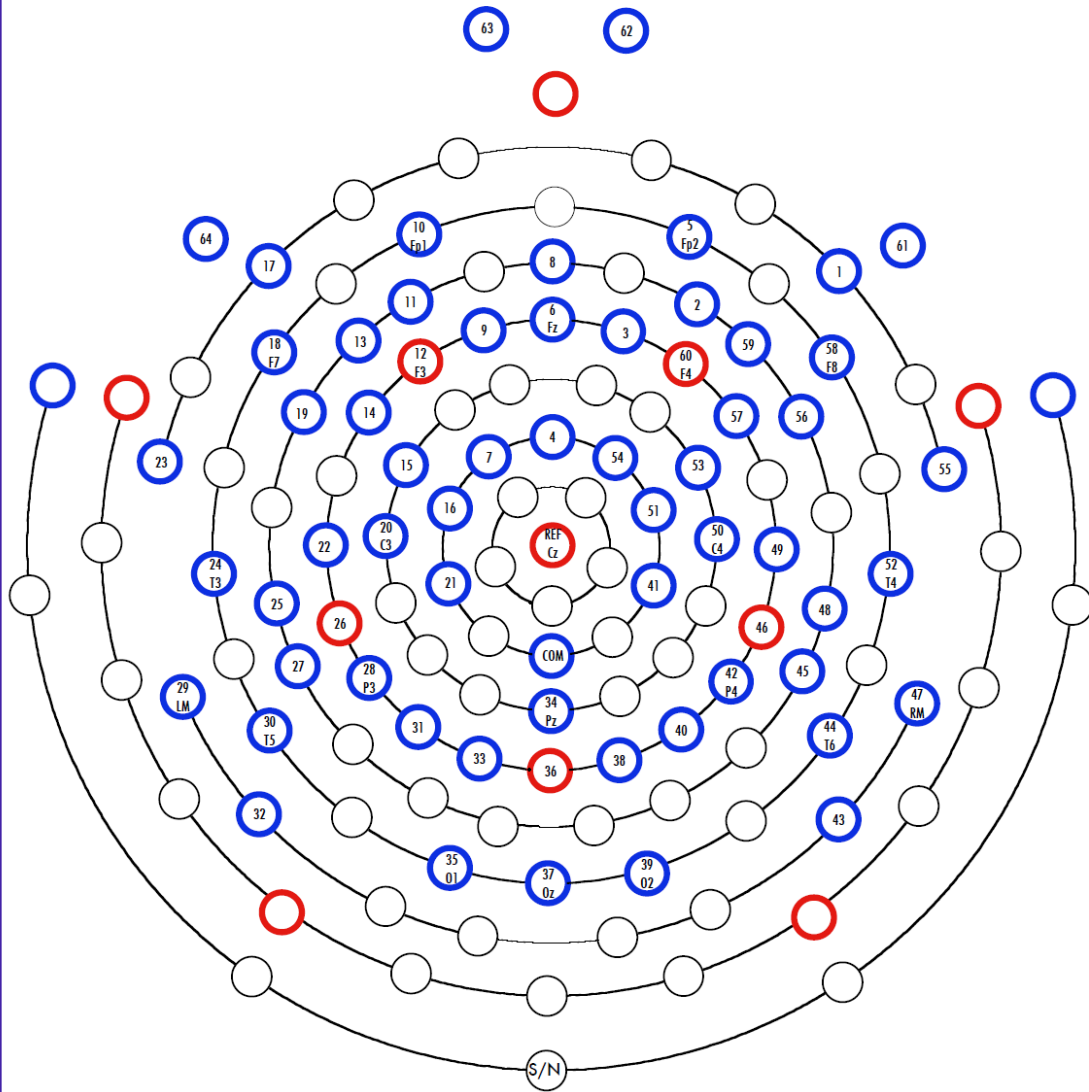
2.2.3 Equipment

The experiment was conducted in a dimly lit, acoustically and electrically sealed room. The participants sat comfortably on a chair facing an LCD display (E2351VR-BN, LG Electronics, Seoul, South Korea) placed on a desk. The screen was approximately 60 cm from the participant. Stimuli were delivered with Presentation Ver. 20.0 (NBS Inc., Berkeley, CA, USA). Participants' responses (finger lifting) were acquired by a capacitance sensor (AD00019, Bit Trade One, Ltd., Sagamihara, Kanagawa Prefecture, Japan). Event triggers were directly synched with the EEG amplifier through a digital I/O (PCIe-6321, National Instruments, Austin, TX, USA) card. A 64-channel sensor net (HCGSN-64, EGI, Amsterdam, The Netherlands) and a corresponding EEG amplifier (Net Amps 200, EGI) were used to record EEG with Cz reference. Electrode impedance was maintained under 50 k Ω as suggested by the manufacturer. The 0.01-200 Hz band-pass filter of the amplifier was applied during the recording. The data were digitized at 500 Hz. Please refer to Figure 2 for the channel locations of the sensor net.

HydroCel Geodesic Sensor Net

64 Channel Map

Version 1.0



For questions or additional assistance please refer to the EGI Sensor Net Technical Manual or contact us at:

Electrical Geodesics, Inc.
1600 Millrace Drive, Suite 307
Eugene, Oregon USA 97403
Phone: (541) 687-7962 Fax: (541) 687-7963
Email: support@egi.com or info@egi.com

N-PRT-LAM-4300-001

Figure 2 Sensor layout of the electroencephalogram sensor net. Screen capture of the PDF version provided by the manufacturer.

2.2.4 Behavioral measurements and analysis

In addition to the four subjects excluded during the EEG analysis, one participant was excluded from the behavioral measures due to data loss. The mean reaction time, task sensitivity index (d'), and response bias (C) were calculated as performance indices. The task sensitivity and response bias are based on signal detection theory (SDT), as this allows the participant's response bias to be differentiated from the task performance (one's ability to detect and discriminate information), which is normally assessed by percent of correct responses (Marques-Teixeira, Barbosa, & Almeida, 2009; Tanner & Swets, 1954). In calculating the SDT indices, congruent success, congruent failure, incongruent failure, and incongruent success were assigned to hit, miss, false alarm, and correct rejection, respectively. A higher d' indicates higher task performance. Response bias C stays at zero when there is no bias at all. The positive value of C indicates a biased response toward the incongruent responses, and similarly for a negative value. Formulas for both indices are shown below:

$$d' = Z_{hit} - Z_{false\ alarm}$$
$$C = -0.5 \times [Z_{hit} + Z_{false\ alarm}],$$

where Z_{hit} is a z -transformed hit rate [hit count/(hit count + miss count)] and $Z_{false\ alarm}$ is a z -transformed false alarm rate [false alarm count / (correct rejection count + false alarm count)] in both equations. The correction of the z -transformation suggested by Macmillan and Creelman was applied where necessary (Macmillan & Creelman, 1991).

2.2.5 EEG analysis

One participant was excluded from further analysis due to malfunction of the equipment. All offline processing of EEG data was carried out using EEGLAB 14.1.2b (Delorme & Makeig, 2004), which is an open-source toolbox of MATLAB software

(Ver. 9.4.0.857798, MathWorks, Inc., Natick, MA, USA). The EEG data were filtered using finite impulse response filters (0.5 Hz high-pass, 40 Hz low-pass, transition bandwidth 1 and 10 Hz, respectively) and epoched according to the stimuli onset. Bad epochs containing fluctuations greater than $\pm 75 \mu\text{V}$ were excluded automatically. All data were then re-referenced to common average reference after omitting outer electrodes (5, 10, 23, 55, and 61–64). Then the clean EEG data underwent adaptive mixture independent component analysis (Delorme, Palmer, Onton, Oostenveld, & Makeig, 2012). Independent components representing eyeblinks or eye movement were manually rejected based on the topography, frequency distribution, and activation synchrony with EOG. After the data cleaning, three participants were excluded from further analysis due to insufficient number of valid trials (valid trials < 25).

Event-related potentials and ERDs were calculated from the same epoch sets selected in the earlier step. The data for observations of left and right fingers were collapsed to focus on the effect of congruency. For ERP analysis, all trials were baseline corrected to the mean amplitude of -100 – 0 ms before onset. For the N2 component, I pooled the potentials at Fz and neighboring electrodes (channels 3, 6, and 9) in the time window from 230 to 270 ms relative to the onset. For the P3 components, activations from 290 to 340 ms were averaged using the same procedure as the N2 component.

Event-related desynchronizations at the central and occipital sites were calculated by EEGLAB's event-related spectrum perturbation analysis function, which employs wavelet analysis starting with 2 cycles and increasing by 0.5 cycles toward higher frequencies. The alpha band power (8–13 Hz) change after stimuli presentation was calculated in dB relative to the baseline period as with ERP, then the central mu power ERD was calculated by averaging the ERD from 300 to 800 ms at the channels located around the central sulcus (channels 16, 20, 21, 41, 50, 51, and Cz). In addition to the central mu power ERD, I calculated the occipital alpha power ERD observed around Oz

and neighboring channels (channels 35, 37, and 39) to take occipital alpha oscillation into account.

2.2.6 Statistical analyses

All statistical analyses were conducted using R version 3.5.1 (R Core Team, 2018). In order to test the effects of condition and congruency on reaction time, repeated measures analysis of variance (rANOVA) with condition (imitation or spatial) and congruency (congruent or incongruent) was conducted. Task sensitivity (d') and response bias (C) were compared by paired t -tests between conditions, in addition to which a one-sample t -test for C was conducted to test whether C shifted from zero. EEG measures were analyzed by rANOVA. For ERPs, rANOVA with condition and congruency as factors was conducted. For ERDs, rANOVA with condition, congruency, and anterior-posterior position as factors was conducted. Pearson's test of correlation was conducted to test whether the congruency effect on ERPs and ERDs were correlated. Congruency effects ($\Delta N2$, $\Delta P3$, and Δ ERDs) were calculated by subtracting the value of the congruent trial from the incongruent trial at each index of each condition. An alpha criterion of 5% was used for all tests.

2.3 Results

2.3.1 Behavioral measures

Figure 3 shows the mean reaction times of all correct responses. The rANOVA showed a significant main effect of congruency, indicating slower reaction times in incongruent trials. The main effect of condition did not reach significance. The interaction of two factors nearly reached significance (Table 1).

Table 1 Results of repeated measures analysis of variance conducted on reaction time

Source	<i>df</i>	<i>F</i> -ratio	<i>p</i> -value	<i>G.eta</i> ²
Condition	1, 21	0.393	0.537	0.002
Congruency	1, 21	18.730	< 0.001 **	0.099
Condition × Congruency	1, 21	3.158	0.090 †	0.002

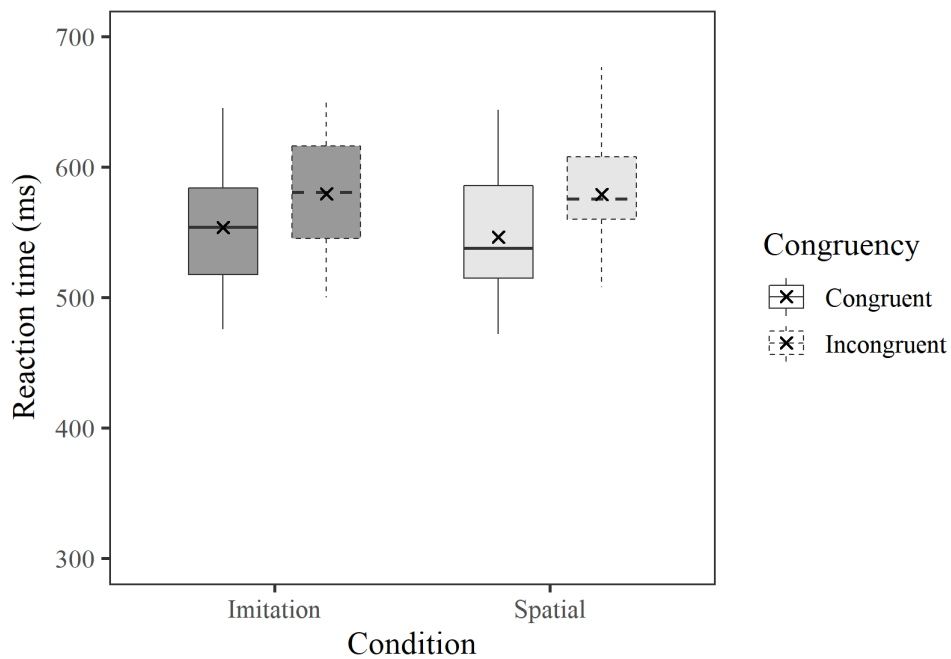


Figure 3 Mean reaction time for all correct responses under each condition and congruency. Mean values are indicated with crosses.

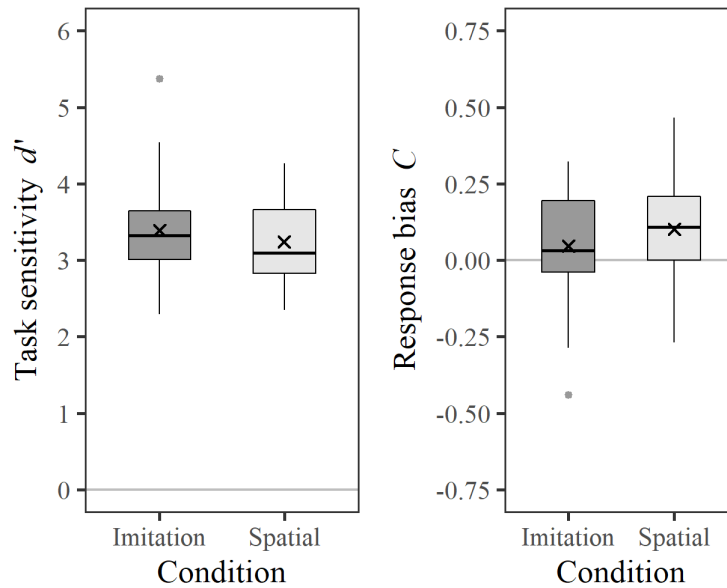


Figure 4 Task sensitivity (d') and response bias (C) at each condition. Mean values are indicated with crosses. Higher d' indicates higher task performance. Positive or negative values of C indicate a response bias toward the incongruent or congruent response, respectively.

Figure 4 shows the task sensitivity and response bias from the behavioral data. The higher task sensitivity indicates more accurate responses by the participants. The operated paired t -test found no statistical difference between conditions [$t(21) = 1.387$, $p = 0.180$], nor did response bias C [$t(21) = -1.120$, $p = 0.275$]; one-sample t -tests showed that the response bias for the spatial condition was biased toward incongruent responses [$t(21) = 2.856$, $p = 0.009$], while no bias was found for imitation condition [$t(21) = 1.112$, $p = 0.279$].

2.3.2 ERPs

Figure 5 shows the grand averaged ERP waveform at each condition and congruency.

The N2 amplitudes at each congruency and each condition are shown in Figure 6. A

rANOVA of N2 amplitude was conducted to test the effects of condition and

congruency. None of the main effects or interaction reached significance (Table 2).

The P3 amplitude at each condition and congruency are shown in Figure 7. None of the

main effects (condition or congruency) or interactions were found significant by the

rANOVA on P3 amplitude (Table 3).

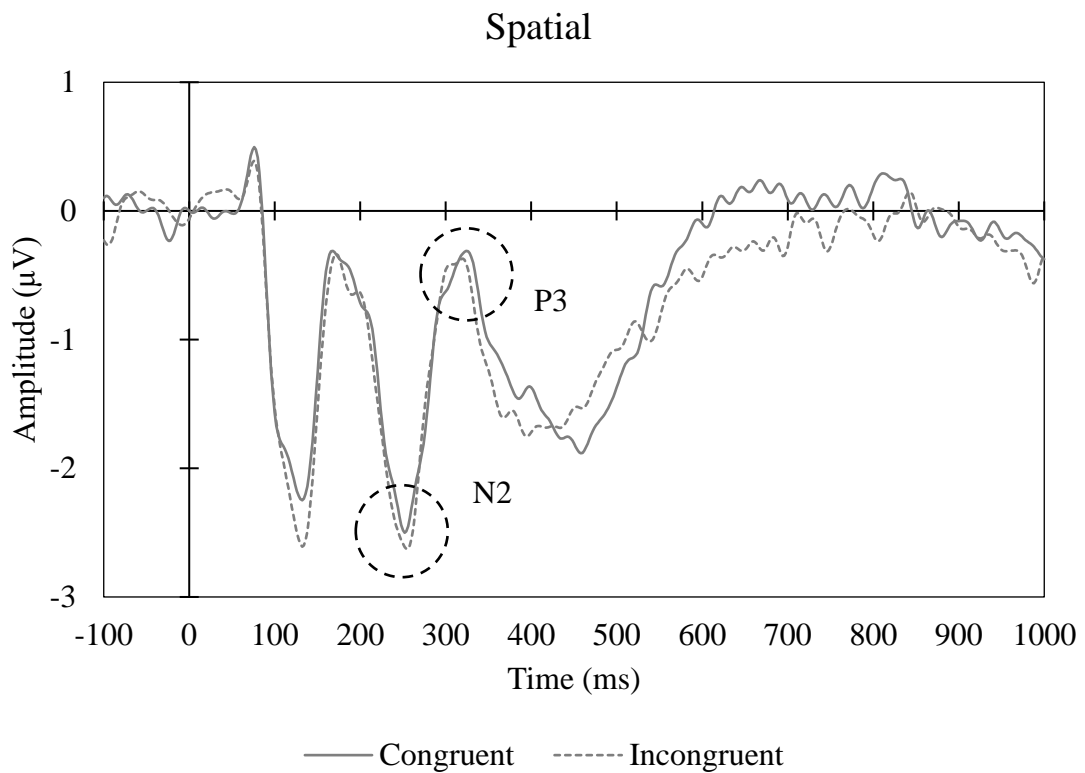
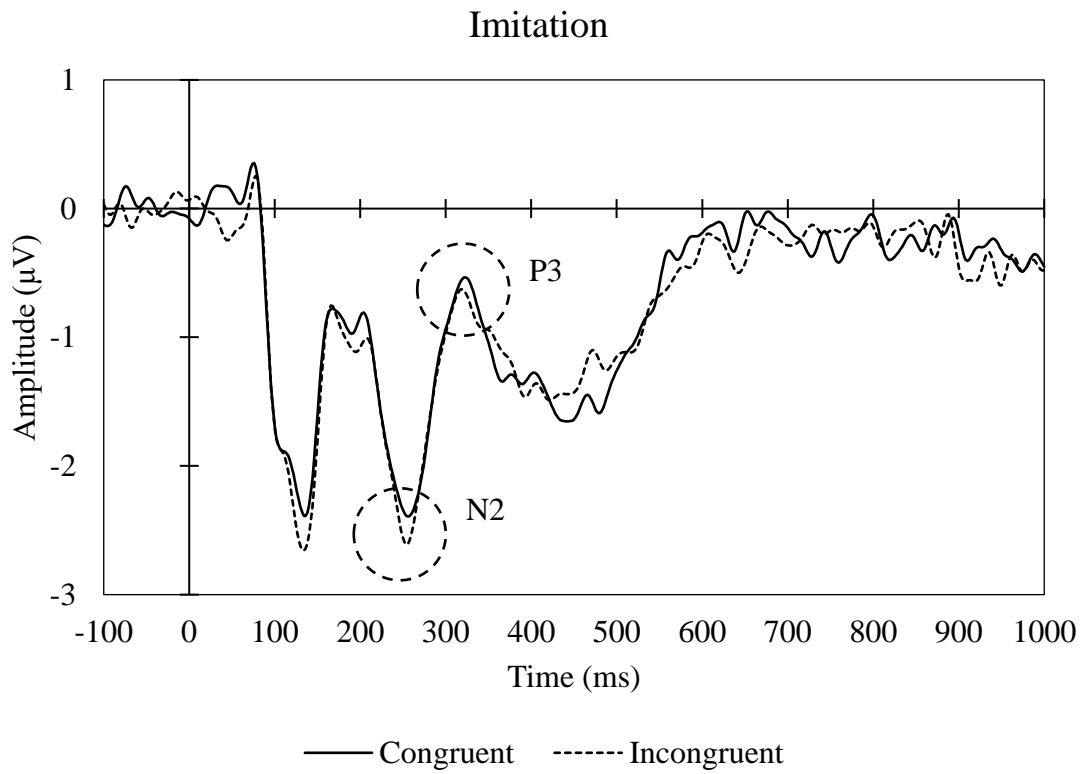


Figure 5 Grand averaged event-related potential waveforms under the imitation condition (upper) and spatial condition (lower) measured around the Fz electrode. Solid line represents congruent trials and dashed line represents incongruent trials.

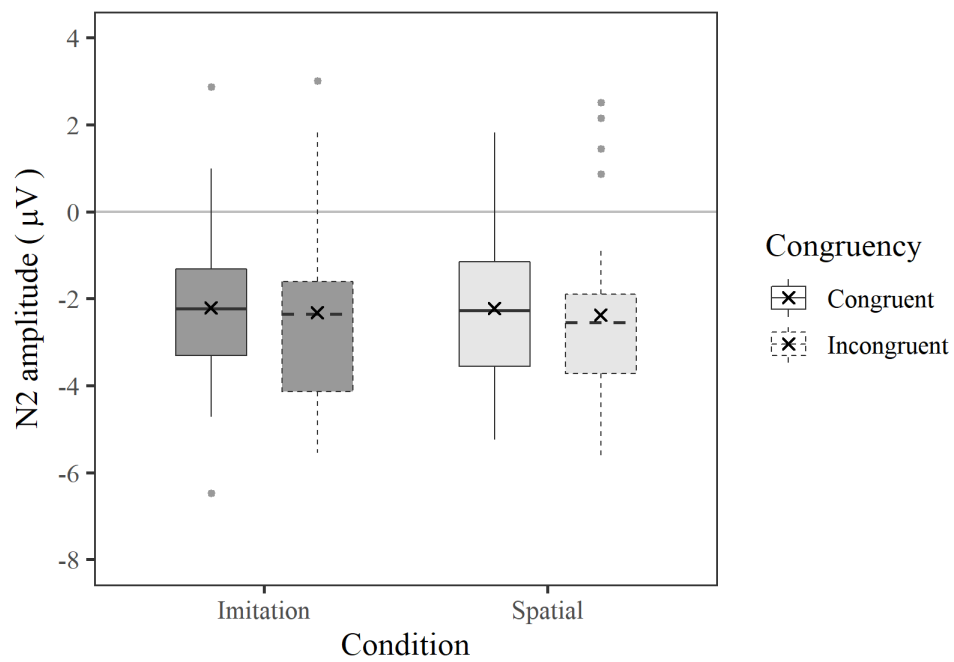


Figure 6 Mean N2 amplitudes under each condition and congruency. Mean values are indicated with crosses.

Table 2 Results of repeated measures analysis of variance conducted on mean N2 amplitude

Source	<i>df</i>	<i>F-ratio</i>	<i>p-value</i>	<i>G.eta²</i>
Condition	1, 22	0.037	0.849	< 0.001
Congruency	1, 22	1.522	0.230	0.001
Condition × Congruency	1, 22	0.040	0.843	< 0.001

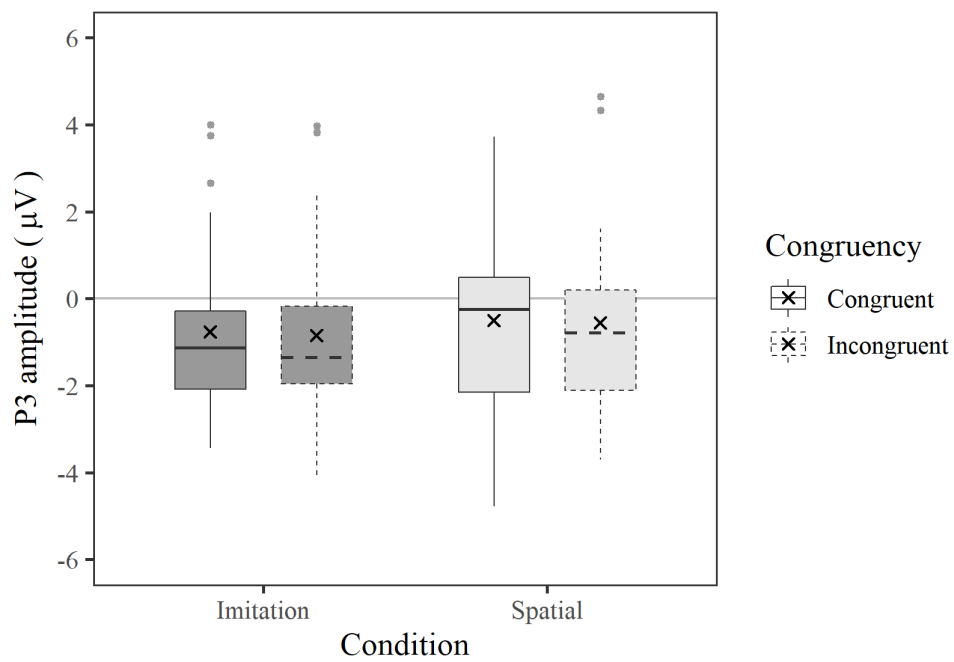


Figure 7 Mean P3 amplitudes under each condition and congruency. Mean values are indicated with crosses.

Table 3 Results of repeated measures analysis of variance conducted on mean P3 amplitude

Source	<i>df</i>	<i>F-ratio</i>	<i>p-value</i>	<i>G.eta</i> ²
Condition	1, 22	2.175	0.155	0.004
Congruency	1, 22	0.314	0.581	< 0.001
Condition × Congruency	1, 22	0.019	0.893	< 0.001

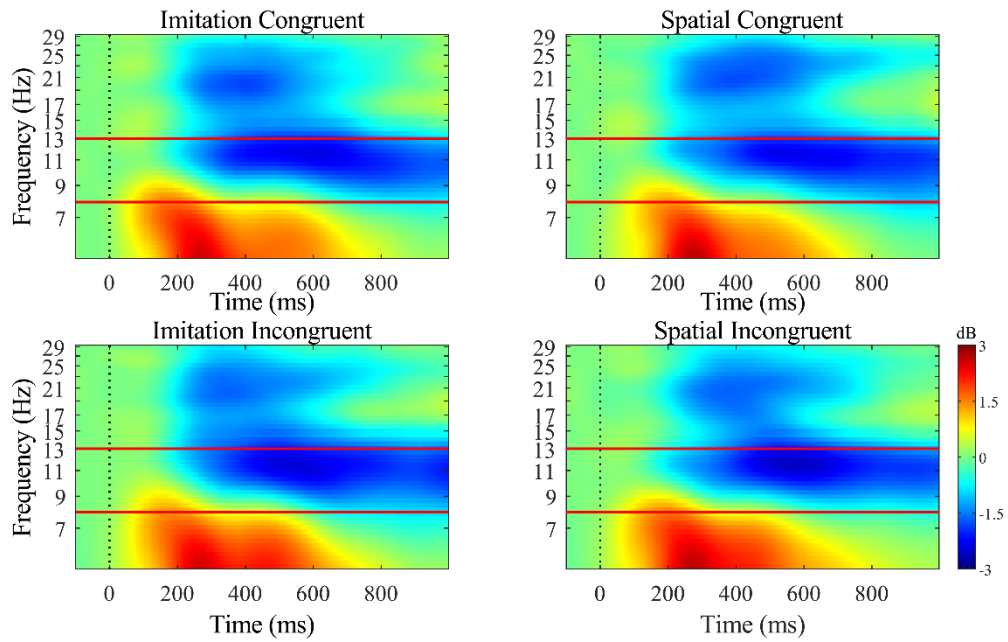
2.3.3 ERDs

The time courses of the grand averaged mu power perturbations relative to the baseline period under each condition and each congruency are shown in the upper half of Figure 8, and the event-related power changes of occipital alpha power are shown in the lower half of Figure 8. One-sample *t*-tests were conducted for all ERDs to test for significant suppression. All ERDs showed significant suppression from the baseline period ($|t_s| > 4.072$, $ps < 0.001$, $n = 23$, for all tests). Figure 9 shows the mean mu and alpha ERD observed at each congruency and condition. Three-way rANOVAs with position (central and occipital), condition (imitation and spatial), and congruency (congruent and incongruent) as factors were conducted on the ERD. A significant main effect of position was found, but no other significant main effect or interactions were found (Table 4). This indicates that the effect of imitative congruency was not found with conditional analysis.

Table 4 Result of repeated measures analysis of variance operated on the event-related desynchronization

Source	<i>df</i>	<i>F-ratio</i>	<i>p-value</i>	<i>G.eta</i> ²
Position	1, 22	8.991	0.007 **	0.036
Condition	1, 22	0.036	0.850	< 0.001
Congruency	1, 22	0.068	0.797	< 0.001
Position × Condition	1, 22	0.081	0.779	< 0.001
Position × Congruency	1, 22	0.243	0.627	< 0.001
Condition × Congruency	1, 22	0.003	0.958	< 0.001
Interaction of all factors	1, 22	0.020	0.889	< 0.001

Central mu ERD



Occipital alpha ERD

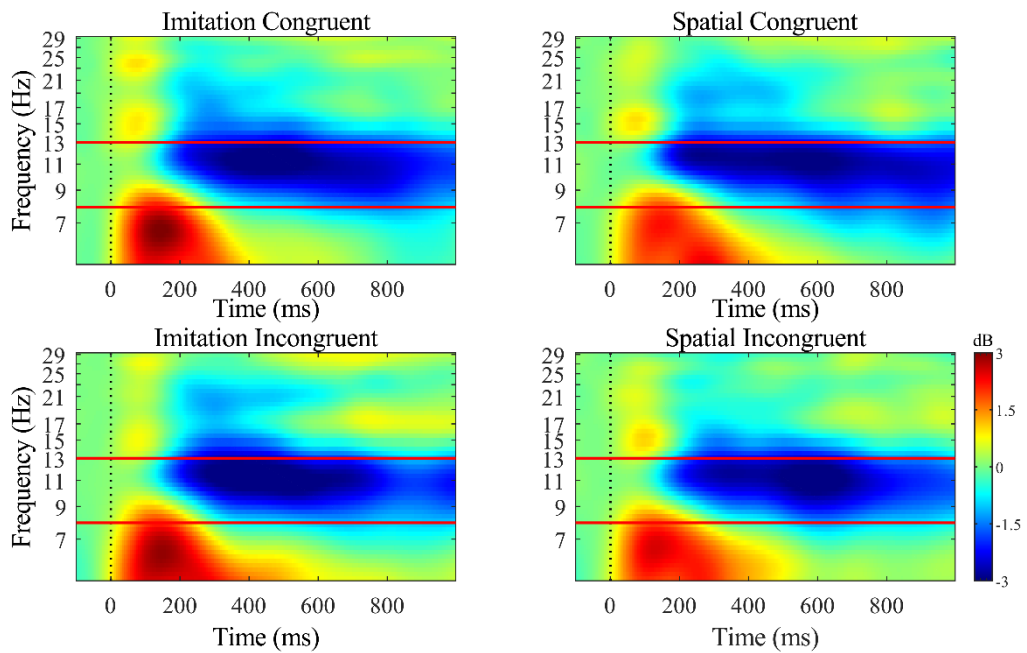
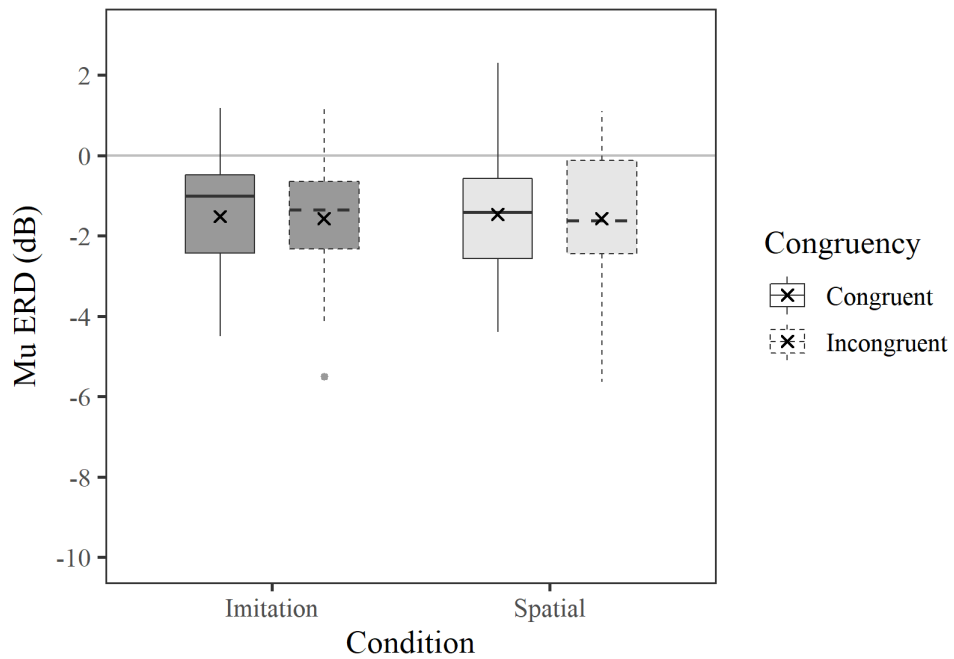


Figure 8 Time courses of the event-related desynchronization of mu (upper) and alpha (lower) wave powers measured over the central sulcus and occipital brain regions. Targeted frequency range (8 – 13 Hz) is indicated by two horizontal lines. Relative power changes from the baseline period are shown in dB. Negative values of ERD are interpreted as stronger cortical excitability.

Central mu ERD



Occipital alpha ERD

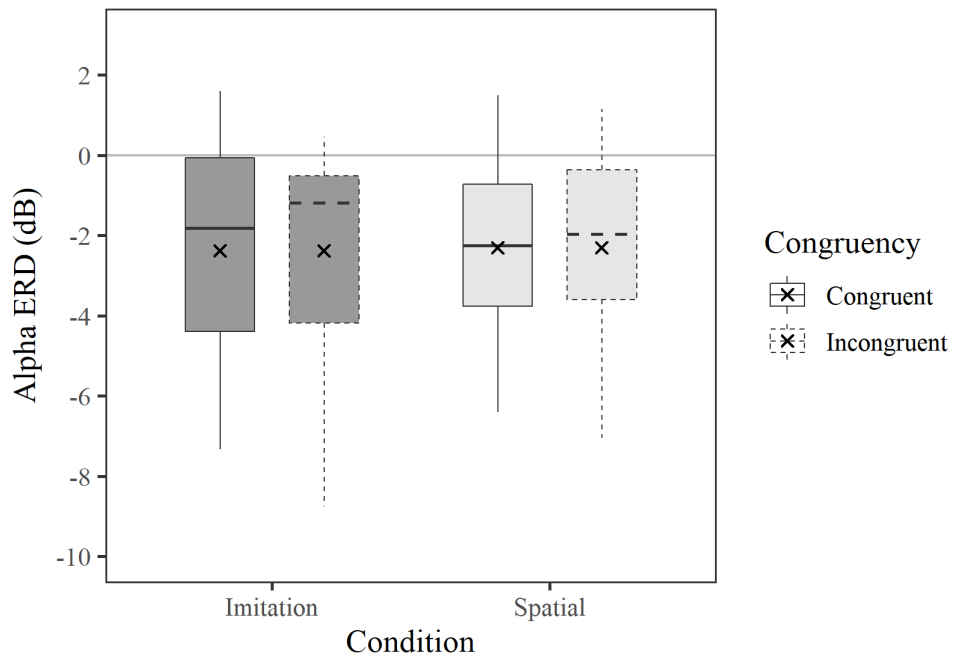


Figure 9 Distributions of mean mu (upper) and alpha (lower) power ERD under each condition and congruency. The more negative the value, the stronger the expected cortical activity.

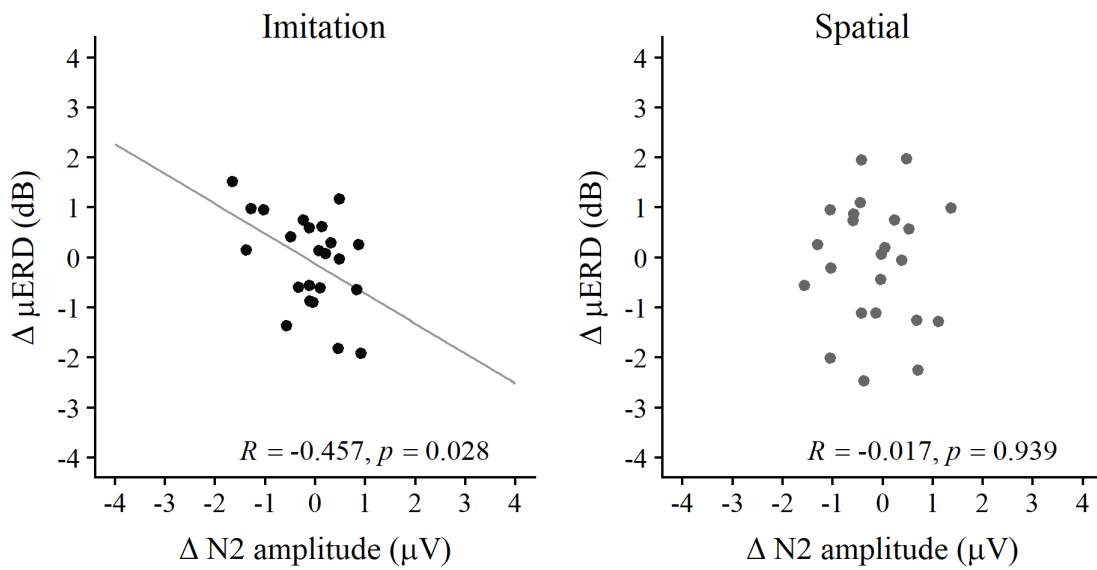
2.3.4 Correlation analysis

The scatter plots in Figure 10 show the correlations between congruency effects on the ERP amplitudes and central mu ERD. There were significant correlations found between $\Delta N2$ and $\Delta \mu$ ERD only under the imitation condition [$R(21) = -0.457, p = 0.028$]. In addition, a marginally significant correlation was also found between $\Delta P3$ and $\Delta \mu$ ERD [$R(21) = -0.394, p = 0.063$].

The scatter plots in Figure 11 show the correlations between congruency effects on the ERP amplitudes and occipital alpha ERD. No significant correlation was found with Δ alpha ERD.

Notably, no significant correlation was found with spatial condition.

Δ N2 amplitude \times Δ central μ ERD



Δ P3 amplitude \times Δ central μ ERD

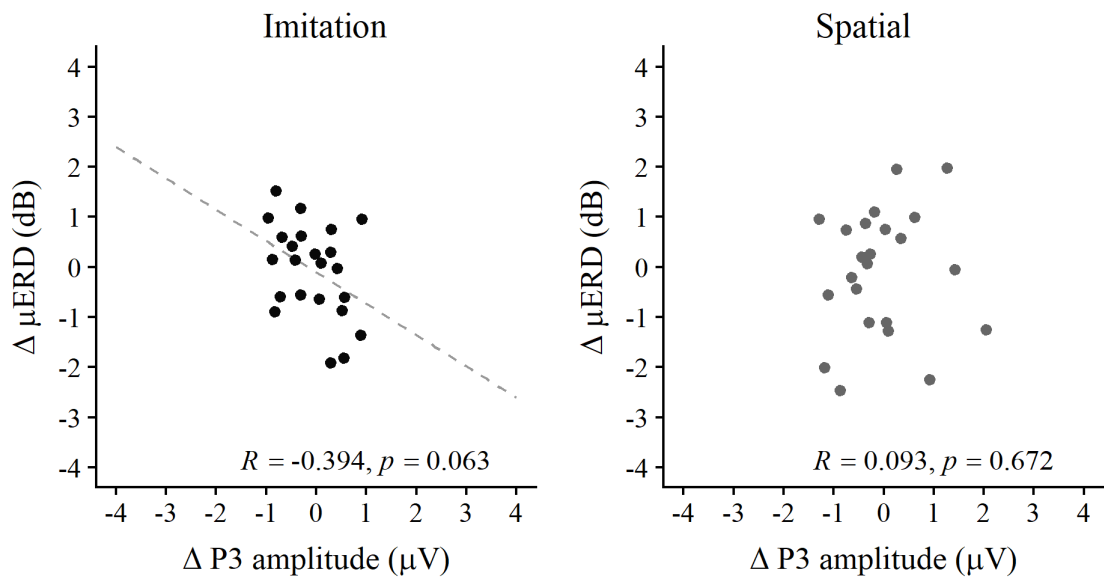
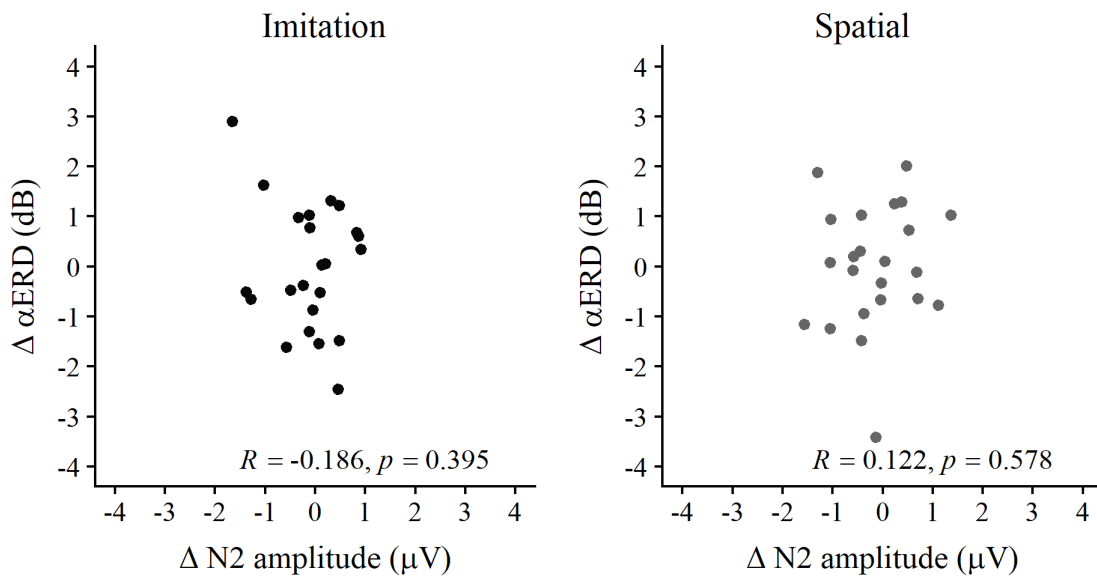


Figure 10 The upper two scatter plots show correlations between Δ central μ ERD and Δ N2 amplitude under each condition. The lower two scatter plots show correlations between Δ central μ ERD and Δ P3 amplitude under each condition. ERD = event-related desynchronization.

Δ N2 amplitude \times Δ occipital α ERD



Δ P3 amplitude \times Δ occipital α ERD

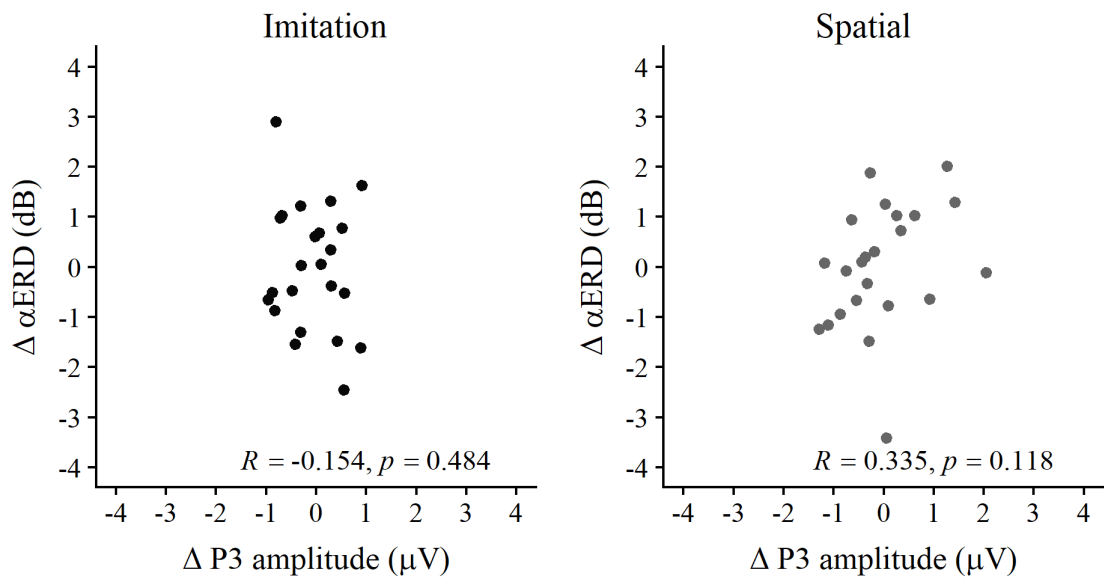


Figure 11 The upper two scatter plots show the correlations between Δ occipital alpha ERD and Δ N2 amplitude under each condition. The lower two scatter plots show the correlations between Δ occipital alpha ERD and Δ P3 amplitude under each condition. ERD = event-related desynchronization.

2.4 Discussion

The present experiment was designed to test whether the N2 and P3 components possibly originating from the frontal brain network are observed during incongruent trials of the task, and if observed, to test their relationship with mu ERD, which is an EEG index of hMNS activity. The N2 and P3 components were observed; however, no effect of imitative congruency on their amplitudes was revealed by a conditional analysis applying rANOVA. Notably, further correlation analysis of the congruency effect on N2 amplitude and mu ERD showed significant negative correlation. Thus, collateral evidence of a functional relationship between the action observation network and the frontal brain network that modulates hMNS activity was found by taking temporal aspects into account.

Reaction times in incongruent trials were slower than in congruent trials in both conditions. This is in line with earlier studies (Brass, Derrfuss, & von Cramon, 2005; Brass et al., 2009, 2001; Campbell et al., 2018; Hazeltine et al., 2000). The task performance, as assessed based on SDT, was relatively high in both experiments. Because there is a tendency for a ceiling effect to manifest itself, the proportion of correct responses is thought less likely to reflect the effect of the congruency (Brass et al., 2005). However, by analyzing the data based on SDT, I found that participants' responses were biased toward the incongruent trials in the imitation condition of Experiment 1. In other words, even in the congruent trials, they responded incongruently. This is likely because the incongruent trial is more difficult than the congruent trial, and thus participants prepared for the incongruent trial while waiting for the next trial. Although direct comparison did not reach significance, it is noteworthy that a significant bias was only observed in the imitation condition.

In the present study, I predicted that the N2 and P3 components, which are well-known ERP components, would be observed during tasks that require response inhibition, and

indeed I found the N2 and P3 components to be elicited under both conditions; however, no congruency effect was indicated by rANOVA. One study conducted a go/no-go task in which a human hand interferes with the participant's selection and reported greater P3 amplitudes in the incongruent trial (Sebanz et al., 2006). However, although the targeted electrode locations were parietal not frontal, Deschrijver et al. reported that the central P3 amplitude in incongruent trials was smaller than in congruent trials (Deschrijver et al., 2017). My result is not consistent with either of these earlier studies. Improvement of the task and study design to capture the effect with the indices used is necessary in the future to gain a comprehensive view.

The congruency effect on mu ERD, an EEG measure of automatic imitation, was tested by rANOVA, which indicated that there was no effect of imitative congruency on the indices. It is known that if inhibition was indicated beforehand, automatic imitation measured by MEP is inhibited during an action observation, but not inhibited if no information was provided (Cross & Iacoboni, 2014b). Although my results are in line with the earlier report, these do not comply with daily life situations. Inhibition of automatic imitation without prior notification is a frequent event. Thus, the absence of the effect on mu ERD might have originated from the S/N ratio of the measure.

Although hMNS activity during the imitation of a hand movement is greater than or at least equal to just an execution of the same action, the change is relatively small (Brihmat et al., 2017; Gatti et al., 2017). In the current study, all responses were made later than 320 ms. Therefore, the mu ERD originating from automatic imitation may be masked by finger lifting, resulting in a reduction in the statistical power of the conditional analysis. Individual differences in inhibition of hMNS are also known to exist (Nishimura, Ikeda, & Higuchi, 2018). Even though it is different from actual response inhibition in some aspects, a task with imaginal imitation and its inhibition may be ideal for focusing on mu suppression originating from hMNS in the future.

Although there was no significant effect of congruency found by rANOVAs on ERPs and ERDs, the relationship between the congruency effect on ERPs and the effect on mu ERD may nonetheless be revealed by taking intra-individual variability into account. Therefore, I calculated the congruency effect on ERPs and ERDs (Δ N2, Δ P3, Δ mu ERD, and Δ alpha ERD) by subtracting the data from congruent trials from those of incongruent trials and applied correlation analysis. The Δ N2 showed significant negative correlations with Δ mu ERD, which was measured later than the ERPs. In addition, Δ P3 showed a trend of negative correlation with Δ mu ERD. The correlations found indicate that those who showed greater frontal activity in incongruent trials successfully inhibited their automatic imitation. This is in line with studies suggesting involvement of the frontal brain regions in imitation-inhibition (Bien et al., 2009; Cross & Iacoboni, 2013; Darda et al., 2018). Importantly, there was no correlation found in the spatial condition. This indicates that these correlations are likely to be related to the processing of imitative compatibility and not to the spatial compatibility. Moreover, correlation analysis for occipital alpha ERD showed no correlations either. This also supports the observed correlation as being more closely related to the processing of human body movement by hMNS (Grèzes et al., 2001; Perrett et al., 1989; Puce & Perrett, 2003) and reduces the concern of a possible contamination by alpha oscillation of mu ERD.

There is ongoing debate over the brain regions or networks responsible for controlling automatic imitation. First, the brain regions known as the “social brain,” such as the temporoparietal junction and dorsolateral prefrontal cortex, were reported to be active during an imitation-inhibition task (Brass et al., 2001; Spengler, von Cramon, & Brass, 2010). In addition, a domain-general MD network responsible for a broad type of reaction-inhibition was also found active during the imitation-inhibition task (Bien et al., 2009; Cross & Iacoboni, 2013; Darda et al., 2018). As several studies have reported that both domain-specific and general brain networks are active during the task,

inhibition of imitation may recruit not only single, but multiple networks for better performance. Because the major source of the N2 and P3 components is located in the domain-general brain regions that inhibit responses (Bekker et al., 2005; Botvinick et al., 1999), the current result is collateral evidence of the involvement of domain-general networks in the task I conducted. Source analysis of ERPs using techniques such as low-resolution brain electromagnetic tomography and dipole fitting with appropriate settings (Delorme et al., 2012; Wagner, Fuchs, & Kastner, 2003) will be useful to overcome the weaknesses of EEG.

In conclusion, in the current experiment, correlations between the imitative congruency effect on ERP and ERD suggest a modulation of automatic imitation by frontal brain activity. However, no significant effect was observed with rANOVAs. Moreover, half of the participants showed an opposite trend from my hypothesis. They showed greater frontal activity and less hMNS activity in the congruent trial. Therefore, a second experiment was conducted applying the following setting: the ratio of incongruent trials was reduced to 25% of the total presentation in order to make the congruent trial more obvious as the standard stimulus and to prevent participants from preparing for incongruent responses.

Chapter 3 Investigating the flexible inhibitory control of automatic imitation using EEG (Experiment 2)

3.1 Introduction

In the previous experiment, the relationship between frontal brain function and hMNS activity was determined by correlation analysis. However, as indicated by the response bias and distribution of congruency effects on ERPs and ERDs, there was a possibility that participants were more prepared for the incongruent trials than the congruent ones. This may have been due to the presentation ratio of congruent and incongruent trials, which was set at 50:50 in the first experiment. In order to suppress the effect of the presentation ratio and to better replicate daily situations, the congruent trial (automatic imitation without inhibition) should be the trial included more frequently, and the incongruent trial should be the one included less. This modification was also expected to enhance the statistical power of the indices. Thus, a change in the presentation ratio may be effective in measuring the effect of imitative congruencies.

In this experiment, a number of incongruent trials were reduced to 25% of the total number of presentations. As in the first experiment, the aim of this experiment was to use EEG to investigate the relationship between the frontal region and hMNS activity during an imitation-inhibition task. Having reduced the number of incongruent trials, I expected participants to prepare more for the congruent trials. In addition, because the N2 and P3 components are known to be more obvious when target stimuli are presented less frequently than the standard stimuli (Donkers & van Boxtel, 2004), the sensitivity of the indices may be enhanced by the task modification. All other aspects of the experimental design were identical to the first experiment.

3.2 Methods

3.2.1 Participants

Twenty-three young adults participated in the study (9 females and 14 males, 23.7 ± 1.8 years). They were recruited from the same population as that of Experiment 1, thus some participants attended both experiments. The Edinburgh Handedness Inventory confirmed that all participants were right-hand dominant. Participants were naive as to the purpose of the experiment and were informed before the study that their privacy would be secure. All participants provided written informed consent prior to the start of the experiment, and they were debriefed following the completion of the experiment. The procedures of the study were approved by the Ethics Committee of Kyushu University. The study was conducted according to the principles of the Declaration of Helsinki.

3.2.2 The imitation-inhibition task

The task employed in the current experiment was basically the same as that in the earlier experiment (see section 2.2.2). However, the presentation ratio of incongruent trials was reduced from 50% to 25%, and the number of congruent trials was increased to 75%. A total of 208 trials were randomly presented (52 incongruent and 156 congruent trials).

3.2.3 Equipment, procedure, and analysis

All of the equipment and procedures in the current experiment were identical to those of the first experiment. All indices were analyzed following the same procedure and using the same methods. The statistical analysis and its criteria were also the same as in Experiment 1. During the data analysis, one participant was excluded due to technical problems and data from four participants were excluded from the final analyses due to insufficient number of valid epochs.

3.3 Results

3.3.1 Behavioral measures

Figure 12 shows the mean reaction times of all correct responses. The rANOVA showed a significant main effect of congruency, indicating greater reaction times in incongruent trials. The main effect of condition and the interaction between the two factors did not reach significance (Table 5).

Table 5 Results of repeated measures analysis of variance conducted on reaction time

Source	<i>df</i>	<i>F-ratio</i>	<i>p-value</i>	<i>G.eta</i> ²
Condition	1, 16	1.801	0.198	0.007
Congruency	1, 16	116.911	< 0.001 ***	0.481
Condition × Congruency	1, 16	0.016	0.901	< 0.001

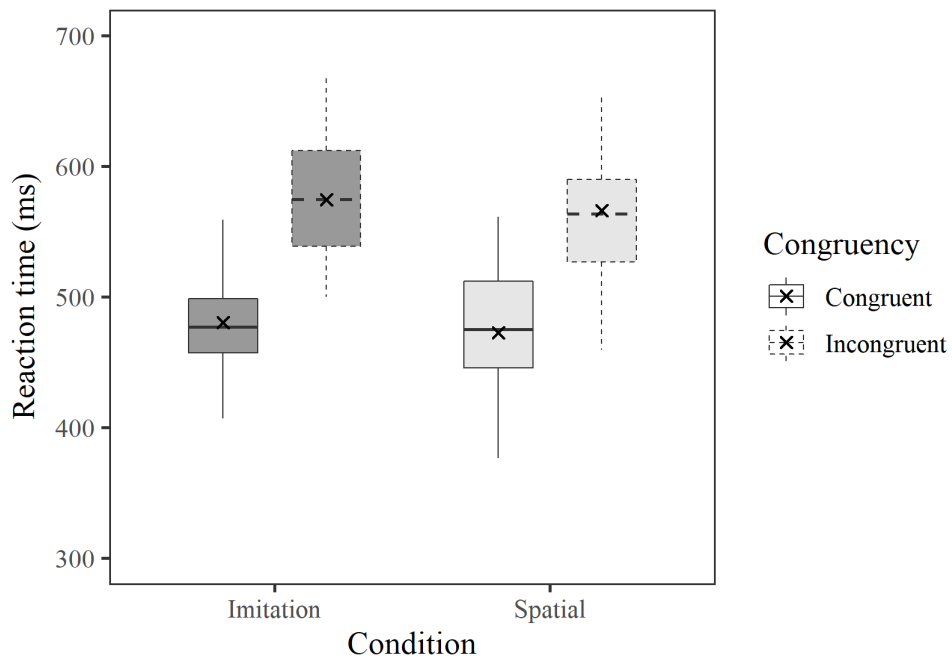


Figure 12 Pooled reaction times for all correct responses in each condition and congruency. Median values are indicated with short lines.

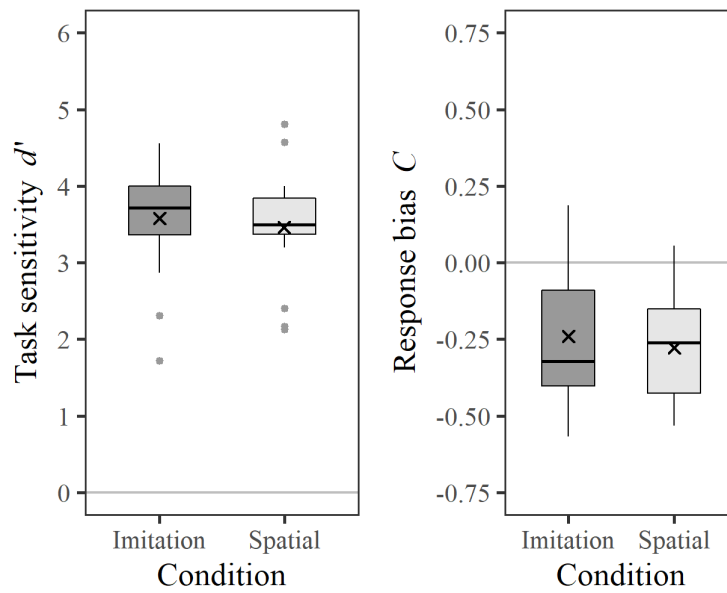


Figure 13 Task sensitivity (d') and response bias (C) under each condition. Higher d' is interpreted as higher task performance. Positive and negative values of C are interpreted as biased responses toward incongruent and congruent responses, respectively.

Figure 13 shows the results for d' and C . No statistically significant difference in task sensitivity was found between conditions [$t(16) = -0.802, p = 0.435$]. The response bias C showed no difference between conditions [$t(16) = 0.647, p = 0.527$], whereas one-sample t -tests showed that the response bias was biased toward the congruent response under both conditions [$t(16) = -4.640, p < 0.001$; $t(16) = -6.468, p < 0.001$; for imitation and spatial conditions, respectively].

3.3.2 ERPs

Figure 14 shows the grand averaged ERP wave form under each congruency and condition. Figure 15 and Figure 16 show the mean amplitudes of the N2 and P3 components at each condition and congruency. The rANOVA of N2 amplitude showed no significant main effect or interaction (Table 6). Similarly, rANOVA of P3 amplitude showed no significant main effect or interaction (Table 7).

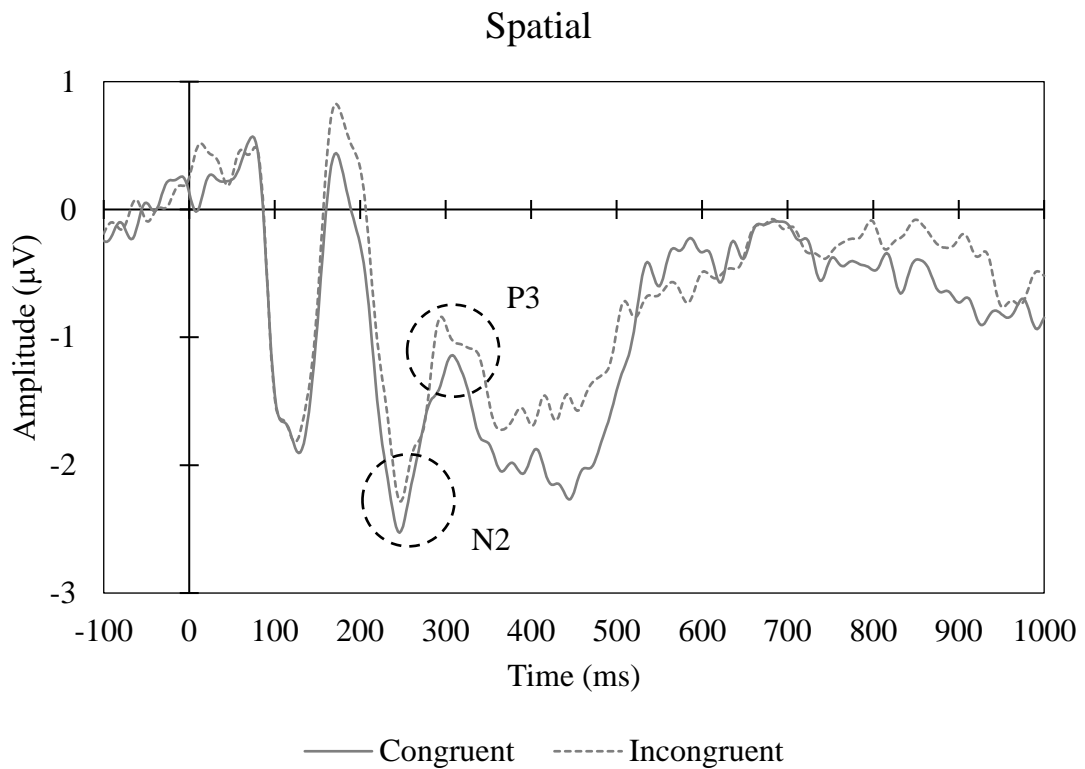
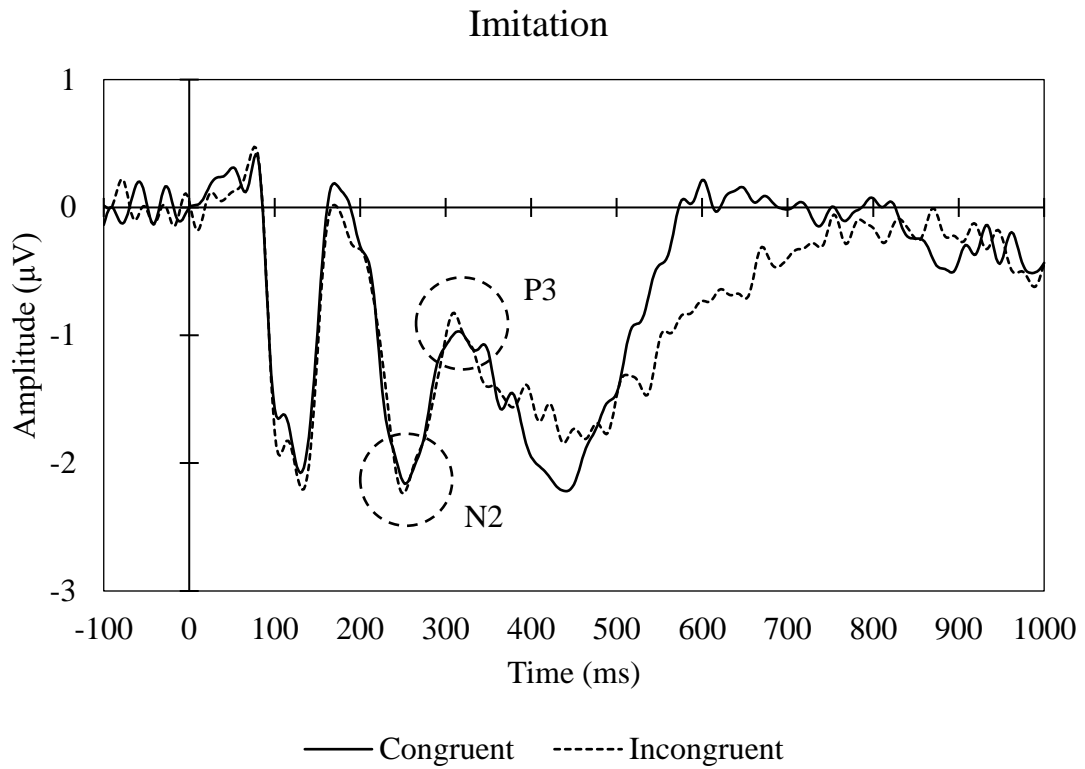


Figure 14 Grand averaged event-related potentials waveforms for the imitation condition (upper) and spatial condition (lower). Solid lines represent congruent trials, and dashed lines represent incongruent trials.

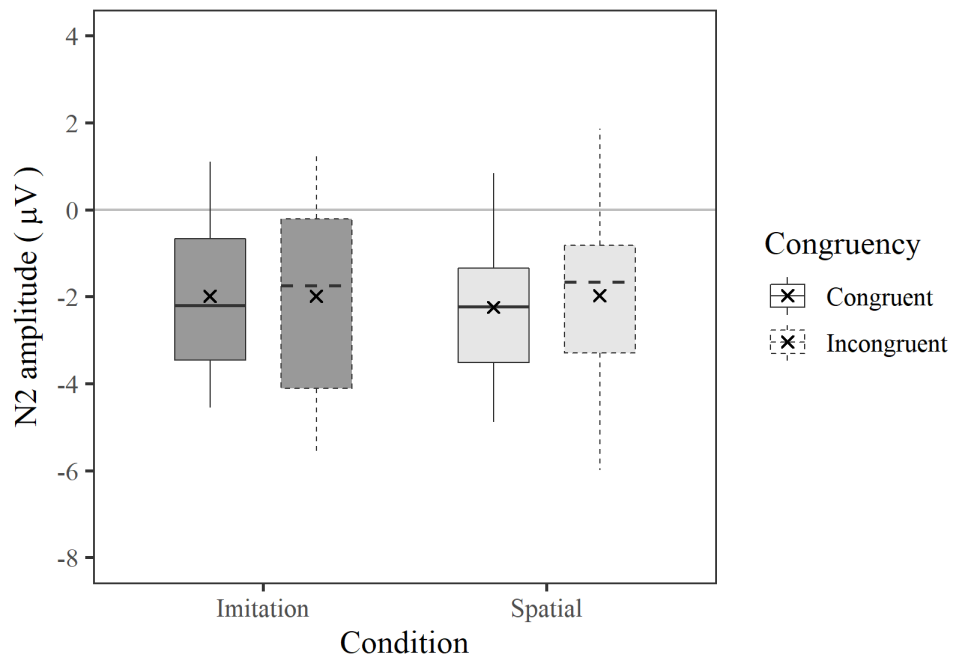


Figure 15 Mean N2 amplitude under each condition and congruency. Mean values are indicated with crosses.

Table 6 Results of repeated measures analysis of variance conducted on mean N2 amplitude

Source	<i>df</i>	<i>F</i> -ratio	<i>p</i> -value	<i>G.eta</i> ²
Condition	1, 17	0.308	0.586	0.001
Congruency	1, 17	0.503	0.488	0.001
Condition × Congruency	1, 17	0.787	0.387	0.001

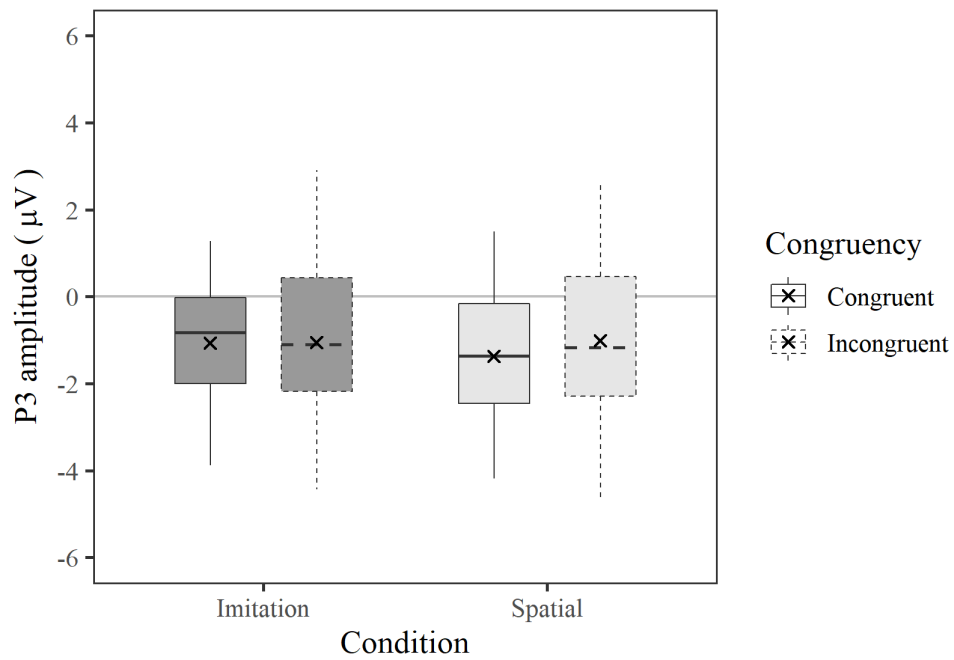


Figure 16 Mean P3 amplitude under each condition and congruency. Mean values are indicated with crosses.

Table 7 Results of repeated measures analysis of variance conducted on mean N2 amplitude

Source	<i>df</i>	<i>F-ratio</i>	<i>p-value</i>	<i>G.eta</i> ²
Condition	1, 17	2.012	0.174	0.002
Congruency	1, 17	0.765	0.394	0.003
Condition × Congruency	1, 17	1.498	0.238	0.002

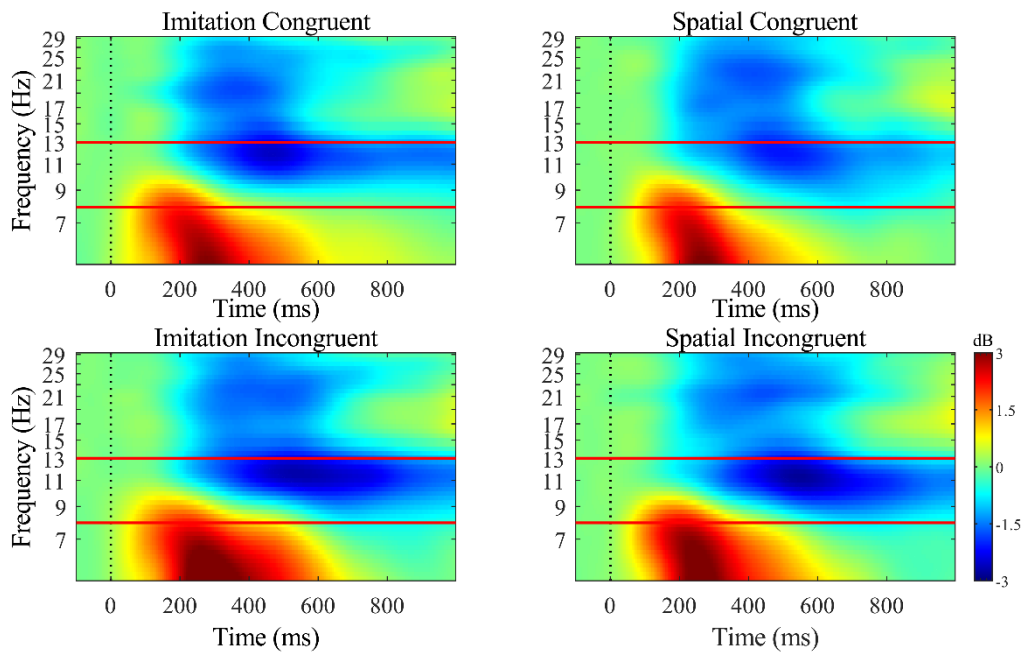
3.3.3 ERDs

Figure 17 shows the time course of the mu and alpha ERD observed under each condition, and Figure 18 shows the distribution of mu and alpha ERD under each condition and congruency. One-sample *t*-tests were conducted for all ERDs to test for significant suppression, and it was found that all ERDs showed significant suppression from the baseline period ($|ts| > 2.202$, $ps < 0.048$, $n = 18$ for all tests). Three-way rANOVAs with position (central and occipital), condition (imitation and spatial), and congruency (congruent and incongruent) as factors conducted on the ERDs found significant main effects of position and congruency. The interaction of position and congruency was also found to be significant. However, the interactions of condition and congruency and of all three factors did not reach the significance that it was hypothesized would be observed (Table 8).

Table 8 Results of repeated measures analysis of variance conducted on event-related desynchronization

Source	<i>df</i>	<i>F</i> -ratio	<i>p</i> -value	<i>G.eta</i> ²
Position	1, 17	8.526	0.010 **	0.018
Condition	1, 17	0.005	0.948	0.010
Congruency	1, 17	6.318	0.022 *	0.010
Position × Condition	1, 17	0.055	0.818	< 0.001
Position × Congruency	1, 17	8.326	0.010 *	0.003
Condition × Congruency	1, 17	1.525	0.234	0.001
Interaction of all factors	1, 17	0.200	0.661	< 0.001

Central mu ERD



Occipital alpha ERD

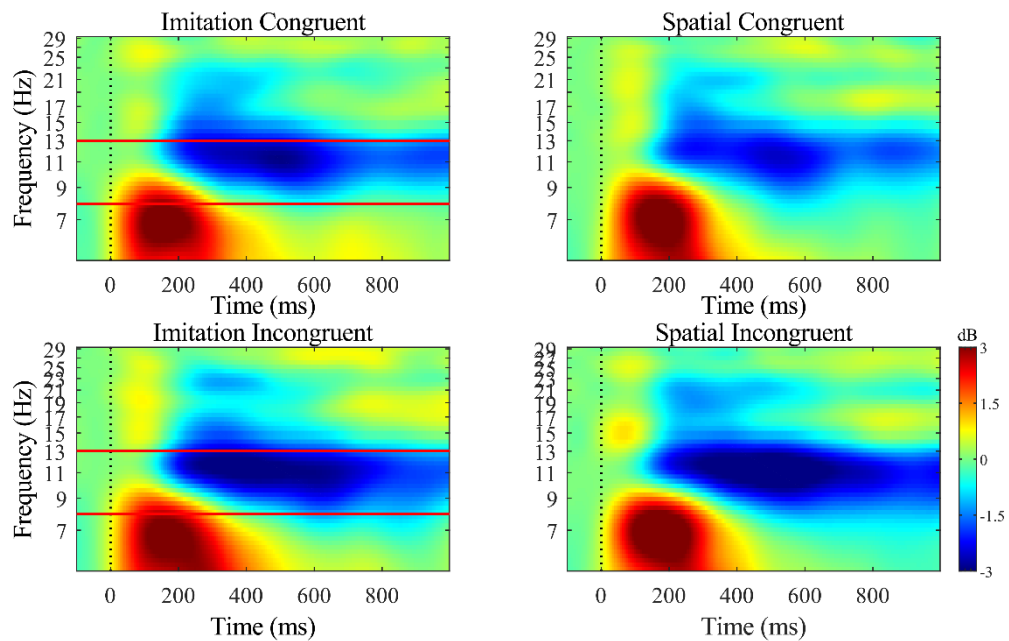
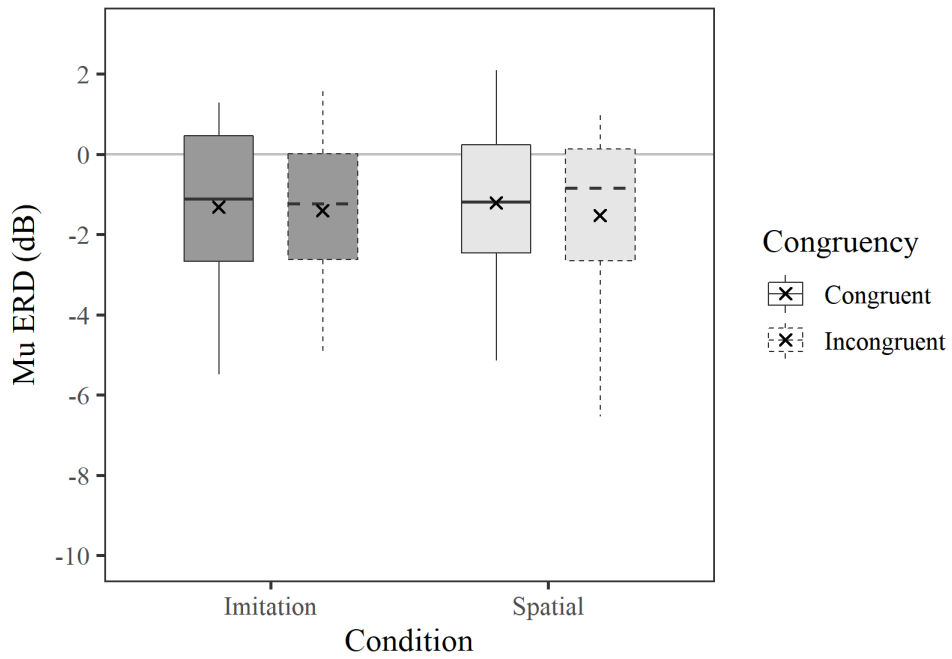


Figure 17 Time courses of the event-related desynchronization of mu (upper) and alpha (lower) wave powers measured over the central sulcus and occipital brain regions. Targeted frequency range (8 – 13 Hz) is indicated by two horizontal lines. Relative power changes from the baseline period are shown in dB. A negative value in event-related desynchronization is interpreted as stronger cortical excitability.

Central mu ERD



Occipital alpha ERD

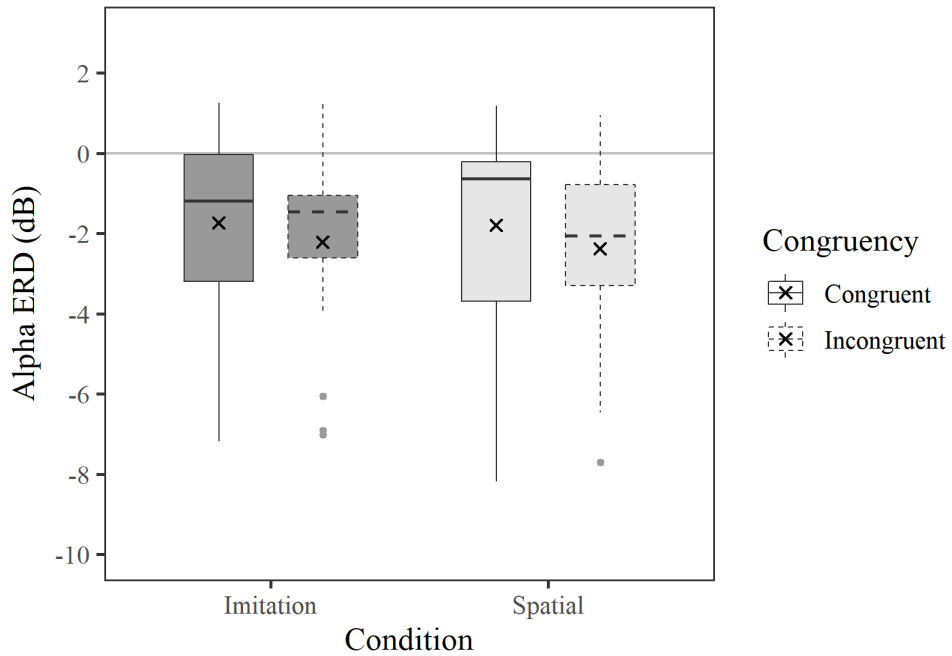


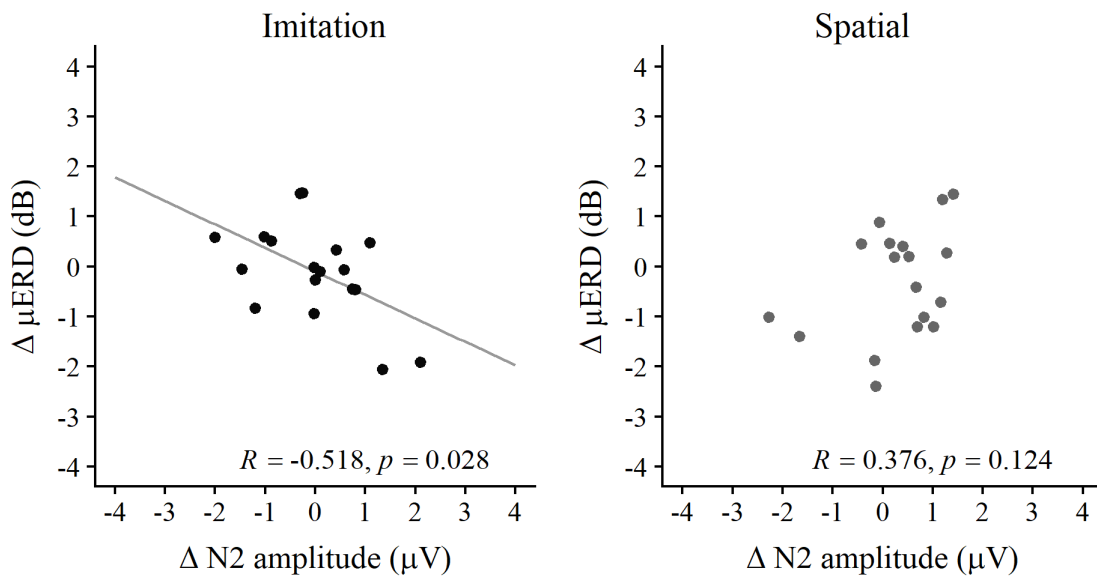
Figure 18 Distributions of mean mu (upper) and alpha (lower) power event-related desynchronization under each condition and congruency. The more negative the value, the stronger the expected cortical activity.

3.3.4 Correlation analysis

The results of the correlation analysis of the effects of congruency on ERPs (Δ N2 and Δ P3) and ERDs (Δ mu and Δ alpha ERD) are shown in Figure 19. Only the negative correlation between Δ N2 and Δ mu ERD was found to be significant [$R(16) = -0.518$, $p = 0.028$], just as in Experiment 1. The trend of a negative correlation between Δ P3 and ERDs found in the previous experiment did not reach significance in the current study.

The results of the correlation analysis of the effects of congruency on ERPs and alpha ERD are shown in Figure 20. No correlation was found in occipital alpha ERD. Notably, no significant correlation was found in the spatial condition.

Δ N2 amplitude \times Δ central μ ERD



Δ P3 amplitude \times Δ central μ ERD

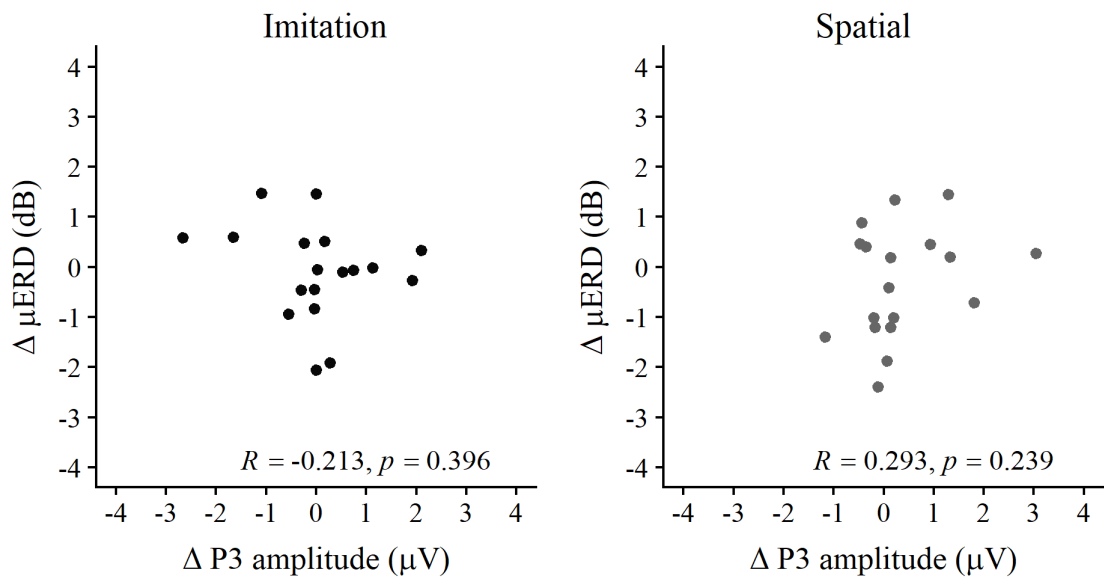
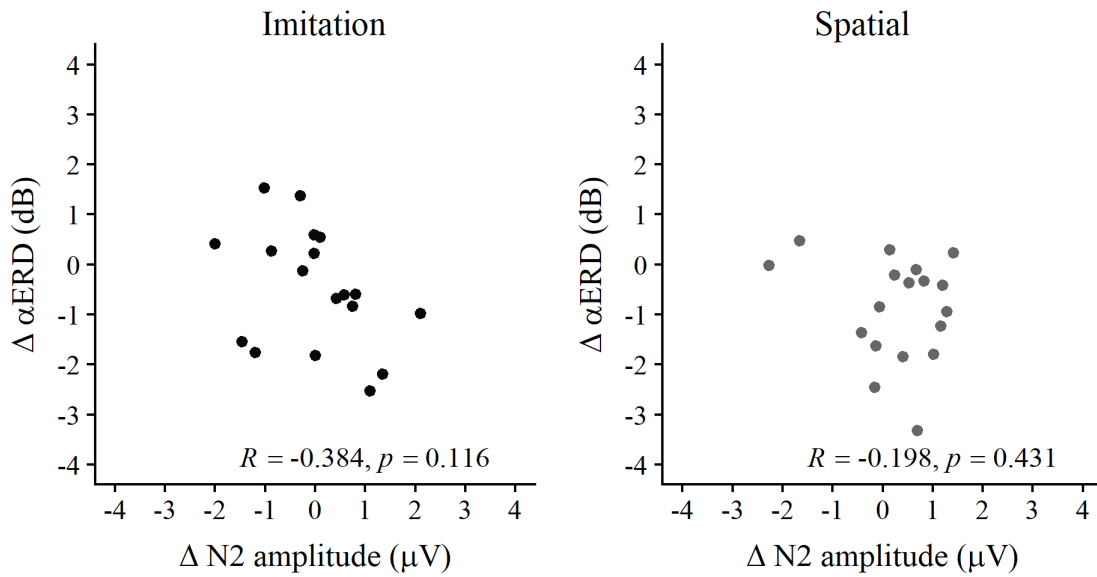


Figure 19 The upper two scatter plots show the correlations between Δ central mu-ERD and Δ N2 amplitude under each condition. The lower two scatter plots show the correlations between Δ central mu-ERD and Δ P3 amplitude under each condition. ERD=event-related desynchronization.

Δ N2 amplitude \times Δ occipital α ERD



Δ P3 amplitude \times Δ occipital α ERD

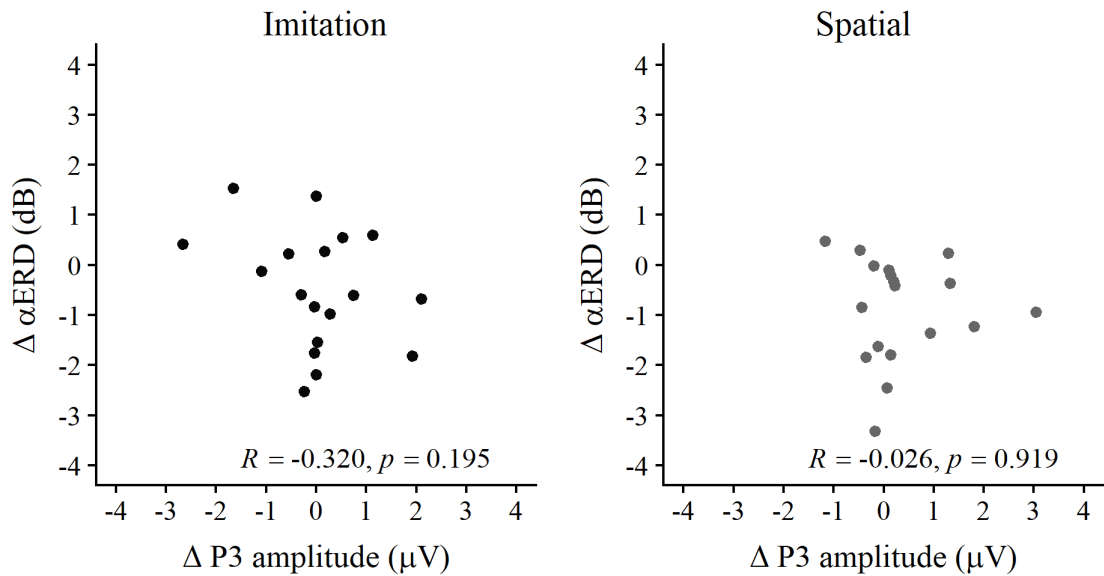


Figure 20 The upper two scatter plots show the correlations between Δ occipital alpha ERD and Δ N2 amplitude under each condition. The lower two scatter plots show the correlations between Δ occipital alpha ERD and Δ P3 amplitude under each condition. ERD= event-related desynchronization.

3.4 Discussion

The present experiment aimed to investigate the contribution of the frontal brain network to the modulation of hMNS activity, which usually works to internally imitate observed actions. As in the earlier experiment, a significant effect of imitative congruency on ERPs and mu ERD was not found by rANOVA even when the presentation ratio was unbalanced. At the same time, the negative correlation between Δ N2 and Δ P3 found in the earlier experiment was also found in the current experiment. Combining these two results from two similar but separately conducted experiments, I may say that a relationship between frontal brain network activity and hMNS activity during the imitation-inhibition task was indicated by EEG.

The results for reaction times showed roughly the same trend as in Experiment 1. A significant main effect of congruency was found, indicating greater RTs in incongruent trials than congruent trials. No significant correlation of two factors was found. By reducing the ratio of incongruent trials from the first experiment, participants were found to respond faster in the congruent trials under both conditions. The response bias C from SDT also indicated that participants were more prepared for the congruent response, thus their response was biased toward congruent responses. The task performance assessed by the task sensitivity d' was high, as indicated in earlier studies and also in Experiment 1 (Brass et al., 2005).

The presentation ratio of go and no-go trials is known to modulate the amplitudes of ERP components (Bekker et al., 2005). However, even when the number of trials was reduced to 25%, no differences between the two types of trials were found with rANOVA. One may claim that the ERP indices that I focused on in the current study did not reflect the inhibitory control of automatic imitation; however, the later correlation analysis revealed a significant correlation. Thus, as suggested by the distribution of Δ N2 and Δ P3, small effect of congruency observed in ANOVA may be originated from

individual differences in brain activation and task strategy. Reconsideration of the task design and additional participants are required in order to reveal the effect of imitative congruency clearly by group level using conditional analysis. The participants were required to respond in both congruent and incongruent trials so as to make the task closer to real life; however, this might also have weakened the size of the effect on the ERP indices. Using the video of the finger just for distraction or to provide information of the required response type in advance, as in earlier studies (Brass et al., 2000; Cross & Iacoboni, 2014a, 2014b; Deschrijver et al., 2017), may be required to focus on inhibitory control using ERPs. Moreover, as suggested in an earlier study using fMRI to investigate the role of the insula cortex in the inhibition of automatic imitation (Campbell et al., 2018), giving four instructions consisting of two congruency instructions (“congruent” or “incongruent” according to the presented action) and two direct instructions (“index” or “middle” regardless of the presented action) may be useful for focusing on imitative congruency.

In the ERD analysis, as already indicated for ERPs, no effect of imitative congruency was observed even in the second experiment. As with ERPs, this may also be due to individual differences, since $\Delta \mu$ ERD showed a wide distribution from the hypothesized positive values to negative values, which is contrary to my preliminary hypothesis. Improvements in the task settings discussed in the previous paragraph may improve the statistical power for ERD as well.

Notably, a negative correlation of $\Delta N2$ and $\Delta \mu$ ERD was found to be significant, as in the first experiment. Because $\Delta \mu$ ERD is measured later than $\Delta N2$, this is collateral evidence for the modulation of hMNS activity by the frontal brain network. Because the first finding was reproduced in the current study, the ratio of incongruent trials is less likely to be the cause of the difference between congruent and incongruent trials. The N2 component elicited by the trials requiring inhibition of response is

believed to reflect the activation of ACC for conflict and behavior monitoring (Bekker et al., 2005; Botvinick et al., 1999). The correlation between the congruency effect on N2 amplitude and mu ERD magnitude was consistent in both experiments. Thus, the anterior part of the cingulate cortex may be related to the spontaneous inhibitory control of automatic imitation. Through the current study, which employed EEG, the temporal aspect of the inhibitory control of automatic imitation has been added to previous findings, which mainly concerned the results of fMRI.

In addition, the negative correlation between Δ P3 amplitude and Δ mu ERD found in the first experiment did not reach significance in this experiment. The P3 component is thought to reflect motor control and inhibition, and its source is located in the medial part of the parietal cortex (Bokura, Yamaguchi, & Kobayashi, 2001; Smith et al., 2008). However, at this time, it cannot be determined whether the correlation found in Experiment 1 was a false positive or not only from the present result.

Although I found the expected correlations, further consideration is needed when interpreting the data. Initially, I expected to observe correlations of the congruency effect just with the degree of the effect on ERPs and ERD. However, the ERP amplitudes of half of the participants were greater in the congruent trials. Similarly, their mu ERD was relatively smaller in the congruent trials. One possibility is the strategy they employed during the task. For example, one may prepare for the congruent response, which is a natural response, while another may prepare for the incongruent trials, which require more resources to comply. Although the response in the current experiment was biased toward congruent responses, some participants showed bias toward incongruent responses. The variation in response bias was also large, suggesting wide individual differences in task pursuance.

In conclusion, the participation of frontal brain activity was further investigated by making a slight change in the task following the first experiment in order to control for

putative individual differences in task strategy and to enhance the effect of imitative congruency on the indices. Although the correlation between Δ N2 amplitude and Δ mu ERD observed under the imitation condition was constantly observed in both experiments, conditional analysis did not reveal any significant effect of imitative congruency on the indices. Thus, the relationship of frontal brain activity and hMNS during inhibition of imitation was indicated by the current experiment; however, a simpler task may be required to control for individual differences in task strategy.

Chapter 4 The relationship between the inhibition
of automatic imitation and personal
cognitive styles (Experiment 3)

4.1 Introduction

As discussed in Section 1.1, by acquiring highly enhanced social abilities, humans built society to survive throughout human evolution (Gazzaniga, 2008). Efficient social cognition is underpinned by the smooth modulation of automatic imitation. Thus, not only automatic imitation but also the flexible modulation of automatic imitation is essential to social cognition (Brass et al., 2009).

According to Decety and Svetlova, empathy is a complex construct consisting of both emotional and cognitive elements (Decety & Svetlova, 2012). As discussed in a previous section (1.6), there has been an attempt to quantify one's personality based on causal cognition. The Empathizing-Systemizing Quotient (EQ-SQ) questionnaire was developed to measure these constructs (Baron-Cohen, Richler, Bisarya, Gurunathan, & Wheelwright, 2003; Baron-Cohen & Wheelwright, 2004). In addition, the Questionnaire Measure of Emotional Empathy, which focuses especially on emotional empathy (Mehrabian & Epstein, 1972), and Interpersonal Reactivity Index (Davis, 1980) are questionnaires widely used to assess personal empathic traits. In the current experiment, in order to focus on the wide range of social cognition in one questionnaire, I adopted the EQ-SQ score to assess an individual's personal traits.

Variation between individuals is known to exist in imitation-inhibition task performance and EQ-SQ scores. However, no study has aimed to address the relationship between an individual's cognitive style (as assessed via the EQ-SQ questionnaire) and flexible imitation-inhibition performance, despite both being closely related to social cognition and interaction in daily life and both possibly originating from higher-order frontal brain functions. By investigating the relationship between personal cognitive traits, assessed by the self-completion questionnaire, and performance on inhibition of automatic imitation, I aimed to deepen our understanding of the involvement of the

inhibiting process of automatic imitation in forming an individual's traits related to social interaction.

To address this, correlation analysis was applied to the behavioral and physiological measures of the imitation-inhibition task and EQ-SQ scores. The mu wave power event-related desynchronization of EEG was chosen for the physiological index of brain activity related to automatic imitation. I hypothesized that participants with a higher EQ would show better performance on the task and successful inhibition of imitative brain activity.

4.2 Methods

4.2.1 Participants

Twenty-six young adults participated in the experiment (15 males, 11 females; mean age = 23.2 ± 1.25 years). All participants were right-hand dominant, as confirmed by the Edinburgh Handedness Inventory (min – max: 70 – 100; median 84.12). They filled out the Japanese version of the EQ-SQ (Wakabayashi et al., 2006) by selecting 1 (“Strongly agree”) to 4 (“Strongly disagree”) for 100 items. Participants were naive as to the purpose of the experiment and were informed before the experiment that their privacy would be secure. Written informed consent was provided by the participants prior to the start of the experiment, and participants were debriefed following the completion of the experiment.

The procedures of the study were approved by the Ethics Committee of Kyushu University. The study was conducted according to the principles of the Declaration of Helsinki.

4.2.2 Equipment

The experiment was conducted in an acoustically and electrically sealed room located at Kyushu University. A 64-channel EEG was recorded using an EEG amplifier (Net Amps 200, EGI) with sensor net (HCGSN-64, EGI). Electrode impedance was maintained below 50 k Ω , as suggested by the manufacturer. Electroencephalogram data were filtered in real time by the amplifier hardware, with the filter set to 0.01 Hz high-pass and 200 Hz low-pass, and digitized at 500 Hz. Stimuli were delivered with Presentation Ver. 20.0 (NBS Inc.) and an LCD display (E2351VR-BN, LG Electronics) refreshing at 60 Hz. Participants’ reactions (finger lifting) were acquired by a capacitance sensor (AD00019, Bit Trade One, LTD.) connected to the Presentation software.

4.2.3 The imitation-inhibition task

The task in the current experiment was identical to the task in Experiments 1. Participants were required to respond as soon as possible according to a simultaneously displayed finger movement and instructions (congruent or incongruent; Figure 1). In addition to the imitation condition, spatial condition was also included. The order of the conditions was counter-balanced. The task was divided into three blocks with a randomization of trials, in which half were congruent and the other half were incongruent (a total of 300 trials; 75 trials each for congruent index finger, congruent middle finger, incongruent index finger, and incongruent middle finger). Left- and right-finger trials were collapsed to focus on the effect of imitative congruency while analyzing the data.

4.2.4 Behavioral measurements and analysis

Reaction time was calculated for each task instruction (congruent or incongruent) under each condition (imitation or spatial). In order to highlight the imitative congruency effect, Δ RT was calculated by subtracting the mean reaction time of congruent trials from the mean reaction of incongruent trials for each condition.

The task sensitivity index (d') and response bias (C) were calculated as performance indices. Please refer to Chapter 2.2.4 for further information on calculation of SDT indices.

4.2.5 EEG measurements and analysis

As an index of automatic imitation, mu wave ERD measured around the central sulcus was acquired by EEG. In addition to mu ERD, alpha ERD, possibly reflecting the attention level, was calculated from the occipital sites in order to take alpha wave contamination of mu ERD into account. All EEG preprocessing and analysis was carried out using EEGLAB 14.1.1b (Delorme & Makeig, 2004), which is an open-

source toolbox of MATLAB (Mathworks Inc). Raw EEG data, following manual rejection of bad channels, were filtered by FIR band-pass filter (0.5–40 Hz; transition bandwidth 1 Hz) and epoched according to stimuli onset. Bad epochs found in the data were automatically rejected according to joint probability of the data (both single-channel and all-channel threshold were set to 3 *SD*). Following this, all data were re-referenced to the common average reference; when the data were re-referenced, the outer electrodes (e.g., facial electrodes) were excluded from the calculation (channels 23, 55, and 61–64). One participant was excluded from further analysis due to an insufficient number of epochs. Preprocessed data then underwent infomax independent component analysis for later artifact rejection (Makeig, Jung, Bell, & Sejnowski, 1996). Independent components representing eyeblinks or eye movement were manually rejected based on the topographical map, frequency spectrum, and activation synchrony with electrooculography.

ERD was calculated using EEGLAB's time-frequency analysis function. First, event-related spectrum perturbations were calculated by wavelet analysis, starting with 2 cycles and increasing by 0.5 cycles toward higher frequencies. Second, mu wave (8–13 Hz) power from 300 ms to 600 ms after the event onset was calculated for each participant in dB relative to the baseline period, which was 200 ms to 0 ms before event onset. Finally, ERDs from each channel were averaged across the regions of interest (ROIs) to improve the reliability of the data. The left central (LC) region, representing mu ERD, was covered by C3 and its neighboring channels (i.e., 15, 16, 20, 21, and 22). The mid-occipital (MO) region, representing alpha ERD, was covered by Oz and its neighboring channels (i.e., 35, 37, and 39). After calculating ERDs, a congruency effect for mu and alpha ERD was calculated in the same manner as Δ RT.

4.2.6 Statistical analyses

In order to test the relationship between the task performance and the EQ-SQ scores, Spearman's rank correlation test was conducted. A Bonferroni correction was used to adjust the p -value for multiple tests. To highlight the effects of task and personal cognitive traits, an additional mixed-design analysis of variance (ANOVA) was conducted on data that showed significant correlations. The factors included in the ANOVAs were high and low groups of EQ or SQ, and congruency (congruent and incongruent). High EQ or SQ groups contained the upper 33% of participants and low EQ or SQ groups the lower 33%. An independent t -test was conducted to test the shift from zero of response bias. All results are reported using an $\alpha < 0.05$. All statistical tests were conducted using R version 3.5.1 (R Core Team, 2018).

4.3 Results

4.3.1 EQ-SQ scores

The EQ and SQ distributions of the participants are shown in Figure 21. Both EQ and SQ varied widely (median = 29, 29; min = 7, 16; max = 58, 64; for EQ and SQ, respectively). No correlation was found between these two scores ($\rho = 0.333$, $n = 25$, $p = 0.103$).

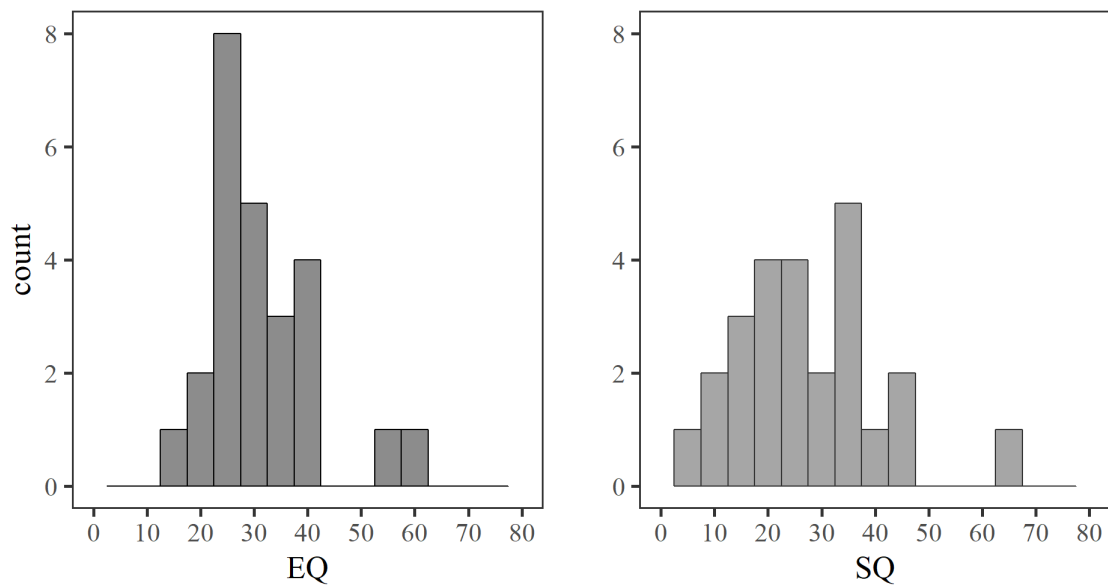


Figure 21 Histograms for the empathy quotient (EQ) and systemizing quotient (SQ) score distributions ($n = 25$).

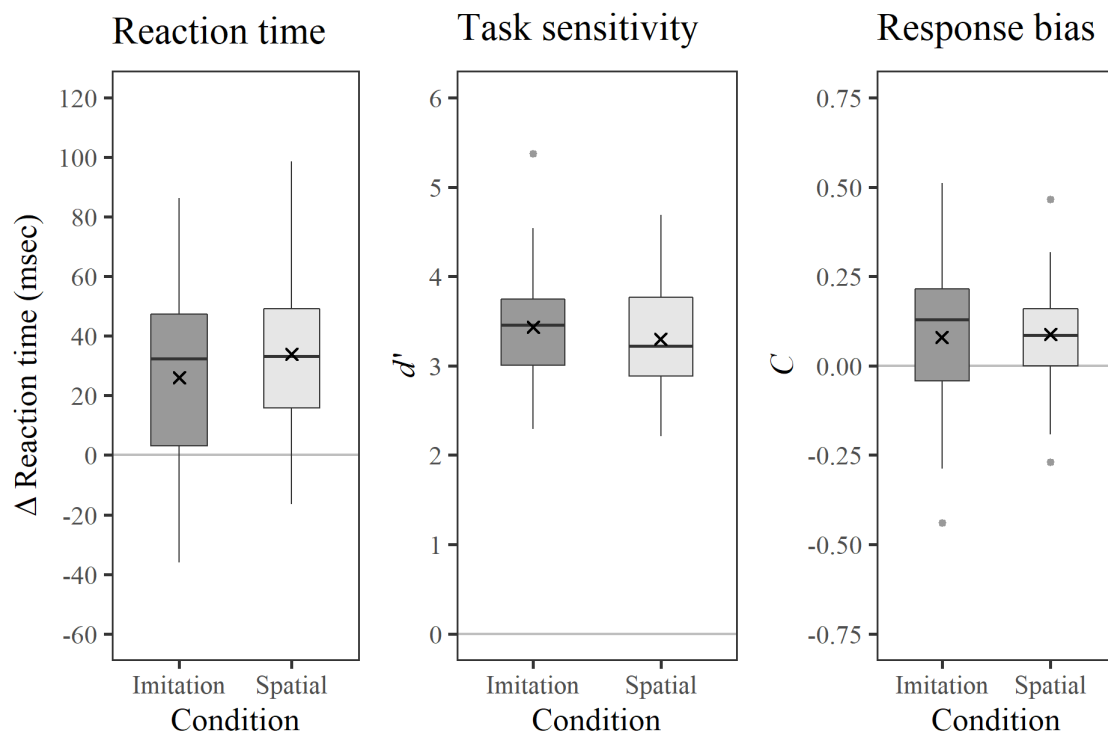


Figure 22 Distributions of Δ RT, task sensitivity (d'), and response bias (C) under each condition. Higher task sensitivity scores indicate higher task performance. A zero value in the response bias indicates that there was no response bias observed.

4.3.2 Behavioral measures

Figure 22 shows the distribution of Δ RT, d' , and C for each condition. Generally, reaction times for the incongruent trials were lower than those for the congruent trials, similar to results reported in earlier studies (Cross & Iacoboni, 2014b). Although task sensitivity (d') was generally high, it ranged from nearly 2 to 5. A one-sample t -test showed that response biases (C) were shifted toward a positive value, indicating that reactions were biased toward incongruent reactions in both the imitation and spatial conditions [$t(24) = 24.582, p < 0.001$; $t(24) = 24.773, p < 0.001$, respectively].

Table 9 Correlations between behavioral indices and EQ-SQ scores

Condition	Index	EQ		SQ	
		ρ	$P_{corrected}$	ρ	$P_{corrected}$
Imitation	Δ RT	-0.43	0.06 †	0.07	1.00
	d'	-0.20	0.68	-0.25	0.45
	C	0.06	1.00	-0.27	0.37
Spatial	Δ RT	-0.29	0.31	0.04	1.00
	d'	-0.43	0.06 †	-0.20	0.69
	C	0.27	0.40	-0.37	0.13

Spearman's rank correlation test.

$n = 25$; Bonferroni corrected: † $p_{corrected} < 0.1$.

The results of a Spearman's correlation test for the behavioral indices are shown in Table 9. Contrary to my hypothesis, negative correlations between EQ and Δ RT in the imitation condition and between EQ and d' in the spatial condition were found, although the p -values did not reach statistical significance after Bonferroni correction. There were no significant correlations found between SQ and behavioral indices.

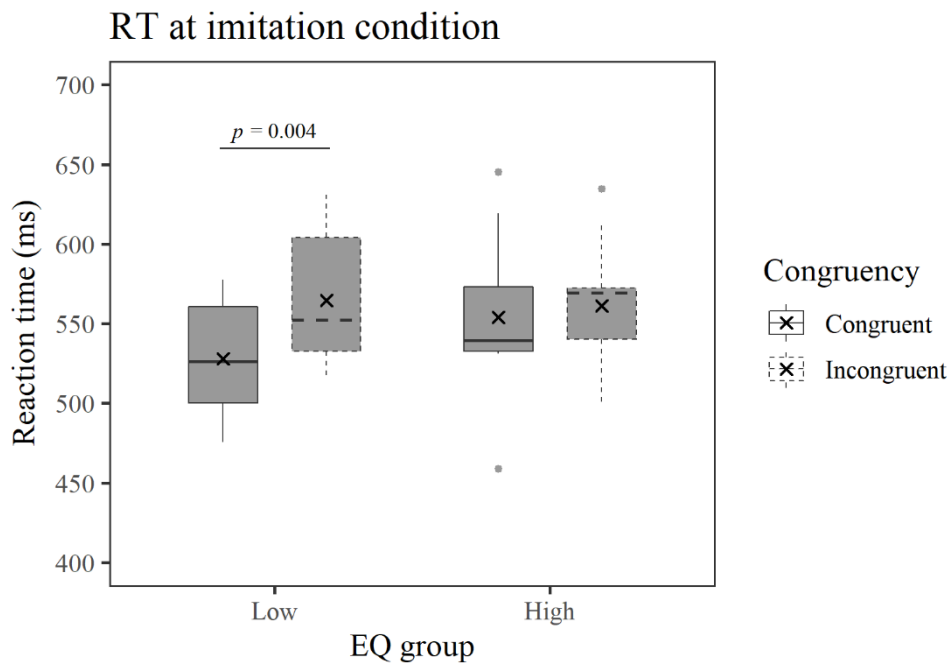


Figure 23 Reaction times under the imitation condition for the low- and high-empathy quotient (EQ) groups.

A supplemental ANOVA on RT measured at imitation condition with congruency (congruent and incongruent) and EQ group (high and low) as factors revealed a significant main effect of congruency [$F(1, 17) = 10.605, p = 0.005, \eta_p^2 = 0.384$], indicating greater RTs in incongruent trials, and an interaction of the two factors [$F(1,17) = 4.785, p = 0.043, \eta_p^2 = 0.220$]. Post-hoc tests on the interaction showed a significant simple main effect of task for the low-EQ group [$F(1,9) = 14.680, p = 0.004, \eta_p^2 = 0.620$], indicating shorter RTs in the congruent trials. However, there were no RT differences in the high-EQ group [$F(1,8) = 0.586, p = 0.466, \eta_p^2 = 0.068$]. As illustrated in Figure 23, the smaller Δ RT in participants with higher EQ was due to slower RTs in the congruent trials.

4.3.3 Physiological measures

Grand averaged mu and alpha ERD waveforms are shown in Figure 24. The distribution of Δ ERD measured over LC (mu ERD) and MO (alpha ERD) are shown in Figure 25. Higher Δ mu ERD indicates a more successful inhibition of hMNS activity during

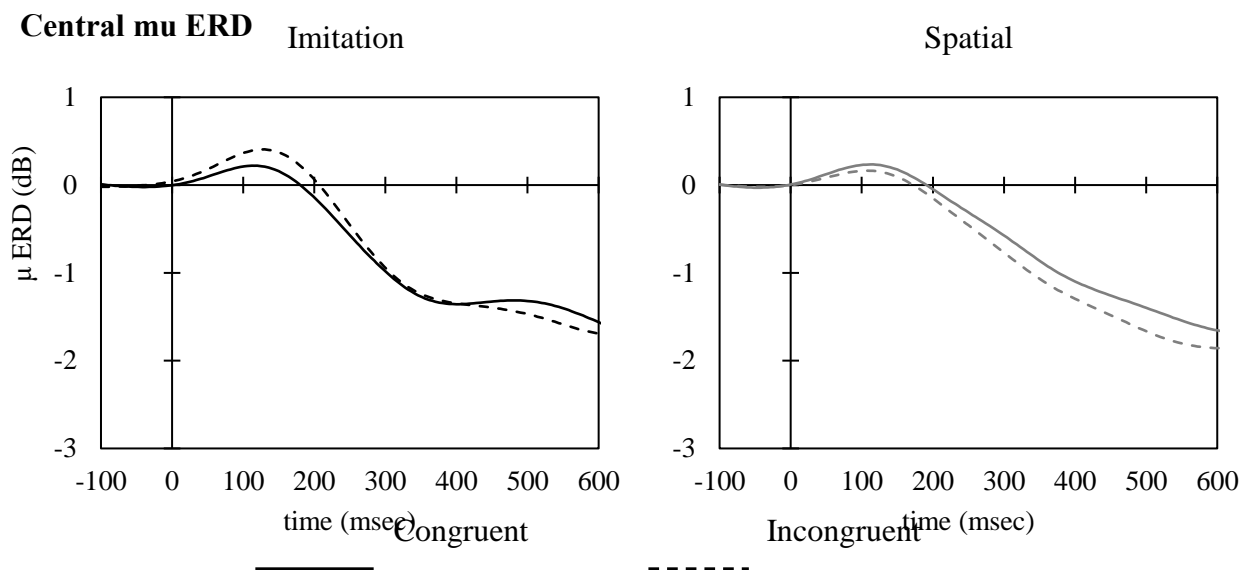
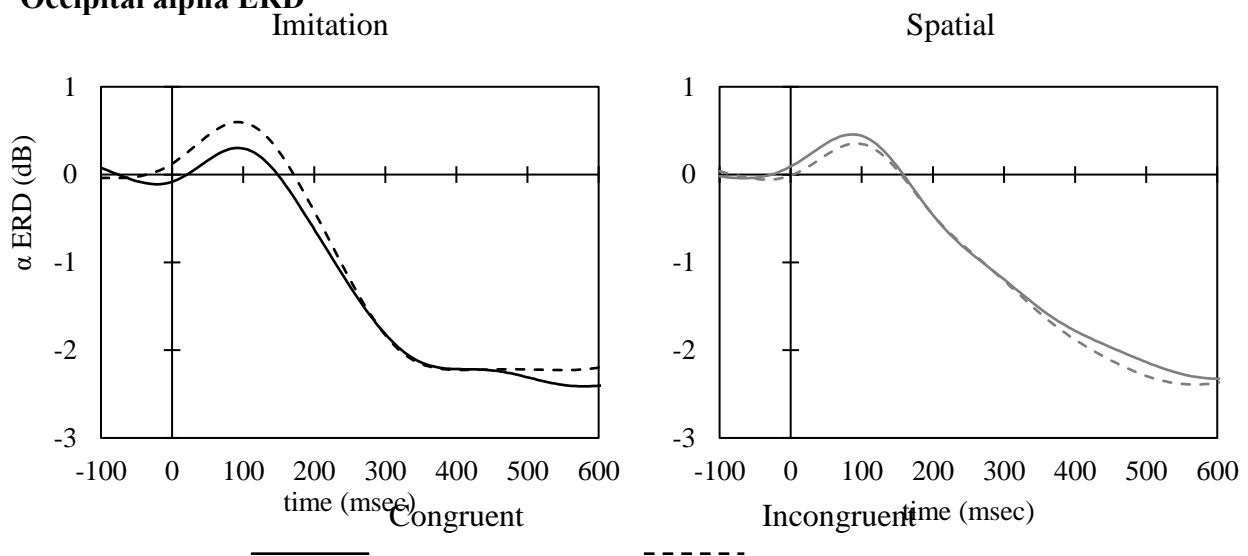
Central mu ERD**Occipital alpha ERD**

Figure 24 Grand averaged mu and alpha ERD under each condition and congruency. ERD = event-related desynchronization.

incongruent trials. Conversely, negative values of $\Delta \mu$ ERD indicate a greater inhibition of hMNS activity during congruent trials. All Δ ERD are distributed from positive to negative values.

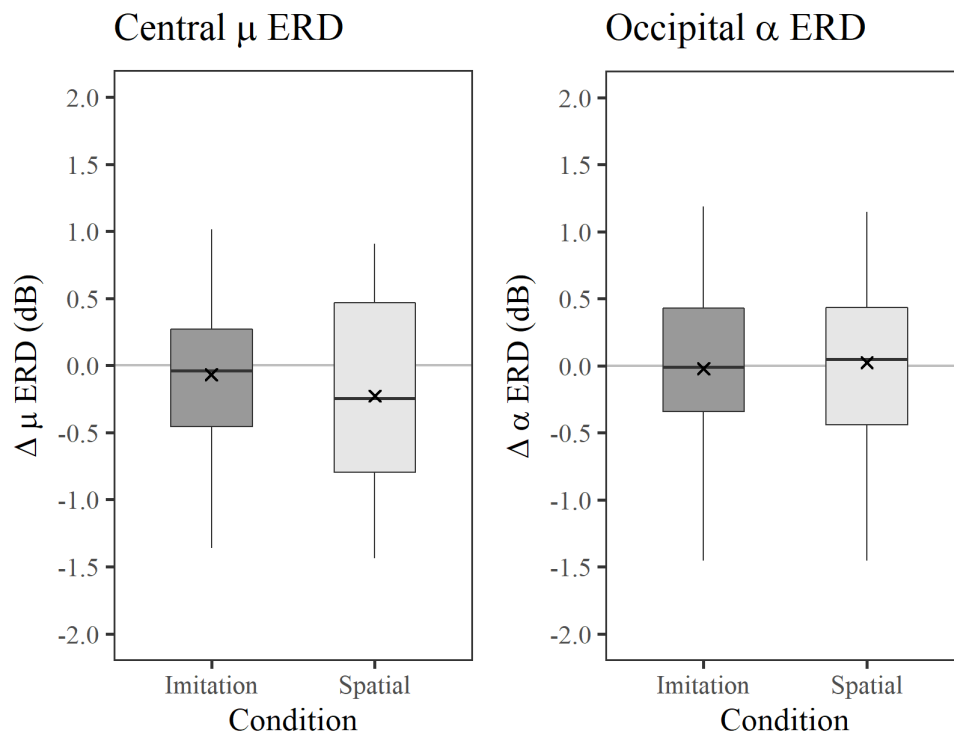


Figure 25 The observed congruency effect on mu and alpha ERD for each condition. Higher values of Δ ERD indicate greater activity during the incongruent trials than the congruent trials. ERD = event-related desynchronization.

The correlation analysis conducted on Δ ERD revealed a positive correlation between SQ and Δ mu ERD in the imitation condition (Table 10).

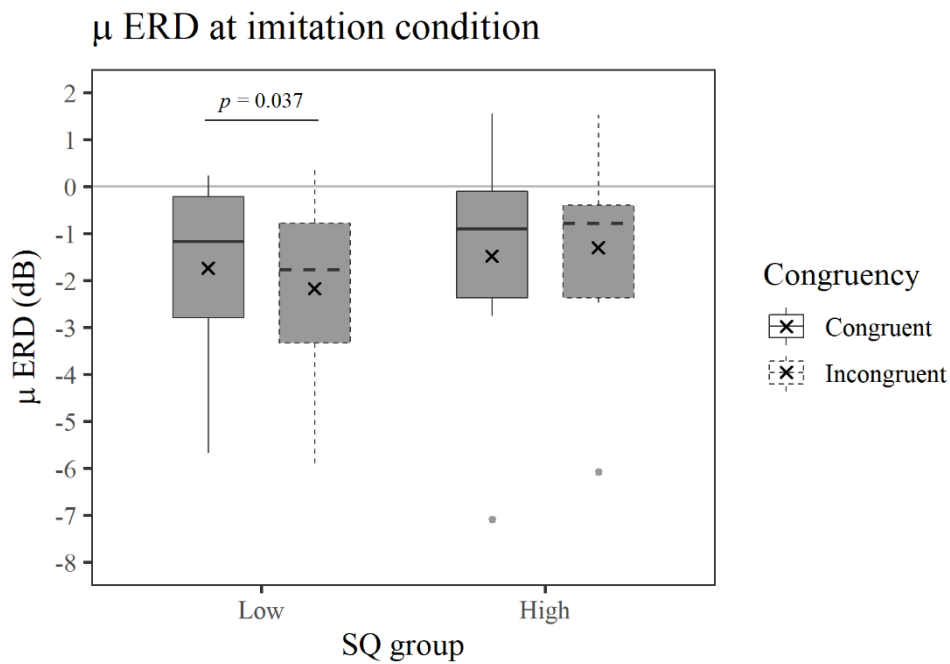


Figure 26 Mu-ERD under the imitation condition for the low and high-SQ groups.

Table 10 Correlations between Δ ERDs and EQ-SQ scores

Condition	ROI	EQ		SQ	
		ρ	$P_{corrected}$	ρ	$P_{corrected}$
Imitation	LC	0.22	0.58	0.46	0.04*
	MO	-0.16	0.88	-0.02	1.00
Spatial	LC	-0.20	0.69	-0.11	1.00
	MO	-0.12	1.00	-0.01	1.00

Spearman's rank correlation test.

ERD = event-related desynchronization; EQ-SQ = Empathizing-Systemizing Quotient questionnaire; ROI = region of interest; LC = left central; MO = mid-occipital.

$n = 25$; Bonferroni corrected: * $p_{corrected} < 0.05$.

An additional ANOVA on ERD measured at LC in the imitation condition with task (congruent and incongruent) and SQ group (high and low) as factors was conducted, showing a significant interaction of the two factors [$F(1,16) = 6.266, p = 0.024, \eta_p^2 = 0.281$]. Post-hoc analysis of the interaction showed a significant simple main effect of

task for the low-SQ group, indicating greater mu suppression in the incongruent trial [$F(1,8) = 6.247, p = 0.037, \eta_p^2 = 0.439$] (Figure 26). No significant correlation was found between EQ and Δ ERDs. In addition, there were no significant correlations found in the spatial condition.

4.4 Discussion

In order to reveal the involvement of the inhibition of imitation on the formation of personal cognitive traits, I tested the relationship between personal cognitive traits and performance on an imitation-inhibition task as measured by behavioral and physiological indices. In the imitation condition, a negative correlation was observed between EQ and Δ RT, although p -values did not reach statistical significance after Bonferroni correction. Moreover, a positive correlation was observed between SQ and the congruency effect as calculated from the mu ERD, which is an EEG index of hMNS activity. As these correlations were specific to the imitation condition, the corresponding correlations in the spatial condition were not significant. In the spatial condition, which was set to take the spatial compatibility effect into account, a trend of correlation between EQ and d' specific to this spatial condition was found. No correlation was found for Δ ERD.

The Δ RT of the imitation condition showed a trend of negative correlations with EQ after correction for multiple tests. A smaller Δ RT can be interpreted as a diminished congruency effect, which can further be interpreted as higher task performance. Nevertheless, in the current study, smaller Δ RTs originated from greater RTs in congruent trials in high-EQ participants, suggesting that they took longer to respond in both congruent and incongruent trials. Therefore, higher empathic cognitive traits may lead to poorer imitation-inhibition performance. From earlier research, it is known that the amount of unconscious imitation is influenced by the amount of rapport felt (Bernieri, 1988; Lafrance & Broadbent, 1976). Moreover, one study, which primed participants either pro- or non-socially and compared the congruency effect under each condition, found that pro-socially primed adults showed a larger compatibility effect in an imitation task (Leighton et al., 2010). Later research also confirmed the effect of priming, especially in adults, compared with adolescents (mean ages around 27 and 13 years, respectively) (Cook & Bird, 2011). Thus, higher empathic traits may disturb

smooth selection (resulting in poorer reaction time) during the imitation-inhibition task. Meanwhile, both empathic traits and higher imitation-inhibition ability are often associated with higher social ability and/or successful interactions (Bozzacchi, Spinelli, Pitzalis, Giusti, & Di Russo, 2015; Iacoboni, 2009; Rizzolatti & Craighero, 2004). Because the correlation found was negative, the current results suggest that a relationship exists between empathic cognitive traits and task performance, but not in a direct manner. Further research investigating this causal relationship is warranted.

There are very few cases where SDT has been used to investigate the inhibition of automatic imitation. A number of earlier studies used Δ RT to highlight the congruency effect of behavioral measures (Brass et al., 2000, 2009; Cross & Iacoboni, 2014b). Compared with reaction times, the error rate is less likely to reflect the effect. Conversely, nominal data contain important information on participants' performance, especially when the data are analyzed in terms of SDT (Barbosa, Almeida, Ferreira-Santos, & Marques-Teixeira, 2016; Marques-Teixeira et al., 2009; Tanner & Swets, 1954). In the current study, the performance index d' showed a correlation with spatial condition, yet response bias (i.e., a shift of decision criterion) did not. No correlations were found between EQ-SQ scores and the SDT measures of the imitation condition. Meanwhile, by analyzing SDT measures, I found that their response was biased toward incongruent responses, indicating that the participants were more prepared for incongruent responses, which require more complete information processing (Brass et al., 2000, 2009; Cross et al., 2013; de Guzman et al., 2016). In this study, I could not find any evidence of a relationship between personal cognitive traits and an individual's task sensitivity or response bias in the imitation condition. However, the use of SDT measures may still provide deeper insights for behavioral data in future research, such as the significant response bias found in the current study. In addition, task sensitivity in the spatial condition showed a marginal negative correlation with EQ scores. This suggests poorer task sensitivity in participants who have a higher tendency toward

empathic cognitions. Although the correlation was not hypothesized and did not reach significance, a relationship may exist between the processing of spatial compatibility generated by the stimuli I used and empathizing scores.

In imitation-inhibition tasks, behavioral measures can be defined as the final output of information processing. Therefore, I focused on EEG mu power suppression related to the observation of the actions of others. By measuring in-brain action mirroring through the widely used mu ERD (Braadbaart et al., 2013; Oberman et al., 2013; Jaime A Pineda, 2005), I assessed the congruency effect at a lower level of information processing. As a result, there was a significant positive correlation found between Δ mu ERD and SQ scores. However, no correlation between Δ mu ERD and EQ was found. This suggests that participants with higher SQ scores were able to modulate mu suppression during incongruent trials, while individuals with lower SQ scores showed greater hMNS activity in incongruent trials than in congruent trials. Thus, task strategy may differ between individuals with lower and higher SQ scores; however, further study of this possibility is required. There were no correlations found in spatial condition. This suggests that the congruency effect observed in the imitation condition likely originated from the process of automatic imitation activated by the presence of biological motion in the stimuli, not from the actual finger movement.

Notably, there were no significant correlations found for Δ alpha ERD, indicating that personal traits were only correlated with congruency effects observed in sensory motor mu rhythms and not in the occipital alpha rhythm. Moreover, no significant correlation was found for the spatial condition. While the required response was exactly the same across conditions, the absence of biological motion was the factor controlled between the two conditions. This result implies that it is not the ability to handle spatial compatibility but rather the ability to deal with biological incompatibility that is correlated with the personal cognitive traits measured by the EQ-SQ questionnaire.

Measures of Δ mu ERD showed significant correlations with SQ scores, while behavioral measures showed significant correlations with EQ scores. Although EQ and SQ scores are known to be moderately correlated, each score is designed to represent an independent aspect of cognition (Baron-Cohen, 2002; Wakabayashi et al., 2006; Wright & Skagerberg, 2012). In addition, no correlation was found between the two scores in the current study. As discussed earlier, if it is assumed that a behavioral measure is the final outcome of the information processing flow for the inhibition task, the mirroring activity and its inhibitory control would take place at relatively earlier steps. Therefore, the behavioral and physiological indices may reflect different levels of processing for the inhibition of automatic imitation. According to the associative sequence learning model, automatic imitation is mediated by low-level mechanisms (C. Catmur, Walsh, & Heyes, 2009; Heyes, 2010; Heyes, Bird, Johnson, & Haggard, 2005). While behavioral measures reflect the whole process, the congruency effect on ERDs (i.e., Δ ERDs) may reflect not only the level of imitation-inhibition facilitated by higher-order brain functions, but also the lower-level processing of observed actions. In other words, not only empathic cognitive function, but also the systemizing aspect of the cognitive ability of social cognition plays an important role in successful task execution. A number of studies using fMRI to determine the brain network responsible for the inhibition of automatic imitation have been conducted (Brass et al., 2000, 2001; Cross & Iacoboni, 2014b; de Guzman et al., 2016). Combining these methods and personal trait data may provide deeper insight into the topic.

Because of their simplicity and popularity in the scientific field, I used EQ-SQ scores to assess cognitive traits. However, further studies with many different questionnaires, such as the Questionnaire Measure of Emotional Empathy and Interpersonal Reactivity Index, combined with appropriate statistics may provide more robust results. Furthermore, despite mu rhythm suppression being a widely used measure of hMNS activity, there are several concerns about its quality. The major claim concerns

contamination of alpha wave attenuation related to attention and visual input (Fox et al., 2016; Hobson & Bishop, 2016). Although simultaneous measurements of fMRI and EEG have suggested that mu rhythm is a reliable index of hMNS activity, additional research with different methods to assess brain activity is required.

In conclusion, this experiment indicated that the behavioral and physiological measures of an imitation-inhibition task are differentially related to personal cognitive traits. The congruency effect on reaction times obtained from the imitation-inhibition task was negatively correlated with EQ scores, and the physiological index was positively correlated with SQ scores. The application of SDT to the imitation-inhibition paradigm provided a deeper understanding of this field of study. Therefore, the current study indicates that variation in cognition is related to the inhibition of congruency effect produced by finger movements. In addition, it is suggested that the behavioral indices and the Δ ERD reflect different steps of information processing. Further research with different empathizing-systemizing assessment methods and neurophysiological measures is warranted.

Chapter 5 Conclusion

In this thesis, the inhibitory processes of automatic imitation and its individual differences were investigated with EEGs, which are characterized by high temporal resolution and relatively low cost. In the history of human evolution, natural selection has shaped humans to build societies, and helping each other is a major strategy in this endeavor. The social brain serves as the primary brain function involved. More than automatic imitation, the inhibitory control of automatic imitation is essential in the daily social interactions that underlie the ability to build a society. Though the social brain handles much of the processing, from the processing of physical information to the processing of psychological information, automatic imitation and its modulation are more likely to be attributed to the physical side. I aimed to investigate the participation of the frontal brain network in the inhibitory control of automatic imitation using EEG indices with high temporal resolution. In addition, correlations between individual differences in related brain activity and task performance on the one hand and personal cognitive styles on the other were tested to investigate the relationship between cognitive personality and the underlying brain activity. I will conclude this paper by summarizing the previous chapters and discussing future studies that could be conducted in this field.

In the first chapter, I introduced the importance of automatic imitation and its underlying neural mechanism in humans. The human mirror neuron system subserves the core function of action observation and higher-order social cognitions included in the action observation network. Methods to assess hMNS activity using the EEG and its advantages and disadvantages were also discussed. I then discussed the importance of the flexible modulation of automatic imitation. It is easy to imagine that imitation without any modulation, especially in an interactive scene, is maladaptive and unproductive. I further discussed the two major brain networks that are suggested to be responsible for modulating the brain activity. One is known as the domain-specific theory of mind network, the other the domain-general multiple demand network.

Although there is as yet no unified view, one or both networks are employed together according to the demands of imitation-inhibition. The task and psychophysiological measures to conduct a study on imitation-inhibition were also introduced in this chapter. Then I introduced the idea of applying a widely used ERP paradigm with tasks requiring the inhibition of response to investigate the inhibition of imitation by means of EEG. Finally, I introduced the purpose of this study, which was to investigate the participation of the frontal brain network in the inhibition of imitation, and individual differences in its modulating processes.

In Chapter 2, I investigated the applicability of the ERP paradigm in investigating the inhibitory control of imitative responses as Experiment 1. Event-related potentials (N2 and P3) observed over the frontal site for inhibitory frontal brain activity and event-related desynchronizations of mu wave power observed over the central site for hMNS activity were acquired by EEG. In addition to the psychophysiological measures, behavioral indices were assessed by applying signal detection theory to analyze the participants' response more closely. As a result, although the N2 and P3 components were observed by the task, no effect of imitative congruency was found by conditional analysis using rANOVA. In contrast, correlation analysis of the congruency effect on ERPs and mu ERD showed a significant relation between frontal brain activity and "modulated" hMNS activity, which was acquired slightly later than the frontal activity. Thus, the applicability of ERP and ERD to assess the inhibitory control of imitative tendencies was indicated by the experiment; however, individual differences in task strategy and brain activation remained to be controlled to gain deeper insight. To address these issues, the second experiment was conducted.

In Chapter 3, the relationship between frontal brain activity and hMNS during the imitation-inhibition task was further investigated by changing the presentation ratio of congruent and incongruent trials as Experiment 2. The task was designed to enhance the

effect of imitative congruency by reducing the ratio of incongruent trials, allowing participants to prepare for congruent trials, not incongruent ones. The modification was also made because the N2 and P3 amplitudes are known to be enhanced if the event that requires inhibition is presented less than the standard stimuli are presented. Results similar to those of Experiment 1 were obtained. No effect of imitative congruency was observed by ANOVA design analysis, even in Experiment 2. Importantly, the correlation between imitative congruency effects on N2 amplitude and mu ERD was again found to be significant in Experiment 2. Thus, the suggested relation between frontal brain activity and hMNS activity was replicated in Experiment 2. However, variation could not be controlled by the modification made in the second experiment.

In Chapter 4, an explanation of the individual differences in the effect of imitative congruency was attempted by examining variations in social-cognitive styles as Experiment 3. The relationship between the ability of participants to suppress hMNS activity and their social cognitive style was investigated by simple regression analysis. Participants' personal cognitive traits were assessed by the self-assessment EQ-SQ questionnaire, which was developed based on the empathizing-systemizing theory suggested by Baron-Cohen and his colleagues (Wakabayashi et al., 2006). An imitative congruency effect on reaction times was found to be correlated with EQ scores. An additional analysis using ANOVA revealed that high-EQ participants' reaction times were relatively slow regardless of congruency, whereas low-EQ participants showed higher reaction times in congruent trials, which is a normal observation. As a psychophysiological measure, the congruency effect on mu ERD was also analyzed by correlation analysis. It was found that high-SQ participants are good at suppressing hMNS activity during incongruent trials. The other participants failed to suppress hMNS activity in the trials that required its inhibition. In conclusion, it was indicated that behavioral and physiological measures of the imitation-inhibition task are differently related to personal cognitive styles. Further research with different scales for

individual differences and physiological measures may provide deeper insight into this relationship.

Results of the three experiments suggest that the frontal brain network, which is responsible for higher-order information processing, participates in the inhibition of automatic imitation. In addition, individual differences were observed in the task performance and brain activities, part of which were found to be related to personal traits of social cognition. In particular, by increasing the informational value of finger movements in the stimuli, the task was designed to better replicate daily situations than did earlier studies that used finger movement only as a distractor. Moreover, this is the first study to determine the relationship between hMNS activity and its “modulator” with high temporal resolution, a characteristic of EEG. Because the cost to measure brain activity by EEG is lower than the costs of other methods, the current study is expected to expand the repertoire available to this field of study.

Although a functional relationship between two brain networks was indicated, conditional analysis using rANOVA failed to reveal the effect of imitative congruency in all the experiments reported here. In order to reveal the effect of imitative congruency through such an experimental design using rANOVA, further experiments may be effective through task modifications such as changes in the action presented and assigning more dynamic actions such as opening and closing the hand. Revisions of the task instructions, as discussed previously, are another option to be tested in the future (see Section 3.4). As indicated earlier, EEG has a millisecond-order temporal resolution while sacrificing spatial resolution. Future studies should use multiple measures to overcome the issues of temporal and spatial resolution. Currently, the spontaneous recording of EEG and fMRI is widely applied in the academic field. That would provide deeper insights when investigating the flexible modulation of automatic imitation. This

would also be effective in resolving concerns raised against the reliability of mu power change as an index of hMNS activity (Bowman et al., 2017; Hobson & Bishop, 2016).

Research on automatic imitation and its flexible modulation are very important to understanding the neural background of the highly enhanced social traits of humans. Moreover, many psychological disorders show difficulties in social interaction (American Psychiatric Association, 2013; Williams White, Keonig, & Scahill, 2007). Even where these difficulties are not due to the malfunctioning of hMNS and its modulating process, this research may contribute to the relief of patients and even help to reveal the cause of such difficulties. In discussions of the modulation of the mirror-like brain response in both the academic and clinical fields, less attention has been paid to its facilitating side than its inhibiting aspect, as in the current study. To deepen and widen our knowledge of human nature as a social animal, not only one side but both aspects of the modulation in tandem may lead us to new findings on brain processes. There is research using real-time neurofeedback to train the action observation network, especially for ASD patients (Datko, Pineda, & Müller, 2018; Friedrich et al., 2014; Goodman et al., 2018; J. A. Pineda et al., 2008). Combining findings from such studies may also contribute to revealing the neural background of the flexible modulation of imitative brain activity.

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