

Neural dynamics in human imitation revealed by ERP surface topography

Hirokata Fukushima,^{1,CA} Masahiro Hirai,¹ Akiko Arita,¹ Kazunori Kamewari¹ and Kazuo Hiraki^{1,2}

¹Department of General Systems Studies, Graduate School of Arts and Sciences, The University of Tokyo, c/o Dr. K Hiraki, 3-8-1 Komaba, Meguro-ku, Tokyo 153-8902; ²PRESTO, Japan Science and Technology Corporation, Japan

^{CA}Corresponding Author: hirof@ardbeg.c.u-tokyo.ac.jp

Received 22 May 2004; accepted 20 July 2004

To clarify the neural dynamics in human motor imitation, we examined event-related potentials (ERP) for a reaction time task that required responses to an actor's finger motions with identical motions. Compared with a control task (reaction to an LED illumination), the ERP surface topography in the imitative reaction was differentiated at around 120–200 ms post-cueing, showing an early sensitivity to the response hand over the pre-central region. This result suggested

that activities around the motor areas were facilitated in the imitative reaction, which is consistent with recent neuroimaging studies. However, taken together with that there were no differences in reaction times, the early ERP latency of conditional divergence indicated that neural activities related to imitation are visual responses and do not directly lead to motor acceleration. *NeuroReport* 15:2129–2132 © 2004 Lippincott Williams & Wilkins.

Key words: Action observation; Biological motion; Event-related potential (ERP); Imitation; Motion perception; Reaction time task; Surface topography; Visuomotor

INTRODUCTION

Although human motor imitation is considered an essential base for social cognition, the neural circuits involved in imitation for the most part remain to be elucidated, especially in terms of their temporal dynamics. Due to their high temporal resolution, electrophysiological measurements such as electroencephalography (EEG) and magnetoencephalography (MEG) are suitable for examining neural dynamics. However, most of these applications to the studies on imitation or action-observation have only examined the activities of the motor areas using an index of the brain rhythm (normally of frequencies of 10–20 Hz) over the pre-central sites [1,2], and thus the dynamics of neural pathways have not been fully examined. Nishitani and Hari [3] examined imitation of a hand movement with MEG and clarified the time course for activations of several cortical regions, including the inferior frontal cortex. However, as this is one of only a few examples of an imitation study focusing on neural dynamics, additional examinations from other points of view are required.

Most neurological examinations on imitation, including the studies above, have focused on the mirror activities of the neural substrates that are shared by both the processing of motor observations and the execution. However, to reveal the temporal features of the imitation-specific visuomotor pathway, there is no need to maintain these paradigms featuring observation-execution matching of motor repertoires. We have taken another approach, one that focuses on the processing speed of the imitative reaction, and examined the time course of the corresponding neural response in comparison with a control visuomotor task.

As a suitable paradigm for this approach, Tessari *et al.* [4] used a simple reaction time task to behaviorally examine the

temporal features of imitation. They used two kinds of stimuli, an LED flash and the experimenter's finger pressing a button, with the reaction to the latter stimulus considered 'imitative', given that the cueing and responding motions (button pressing) were equivalent. They found a significant shortening of the reaction time for the imitative reaction, although there was no evidence of a difference in the subjective awareness of the cue timing. Their conclusion was that an imitative reaction should be subconsciously facilitated by specific neural pathways, though the neural correlates of that distinction have yet to be clarified.

Such a mental chronometry paradigm is also suitable for examining neural dynamics; therefore in this study we have employed the reaction time task of Tessari *et al.* with additional controls for the visual stimuli, and measured the corresponding neural dynamics using event-related potentials (ERP). Although the ERP method has practical advantages for examining social activities due to its relative convenience, and also tolerance to the subjects' movement or posture, to our knowledge it has possibly never been used in imitation research. Thus, the present ERP analysis was conducted exploratively; together with behavioral measurements of reaction time, we examined the time course of the ERP surface topography to reveal both spatial and temporal loci of distinction in the visuomotor pathways between imitative and non-imitative reactions.

MATERIALS AND METHODS

Subjects: Twelve healthy, right-handed paid subjects (three females, aged 22–29 years) participated in the experiment. The hand preferences of the subjects were assessed using an abridged version of the Edinburgh

Inventory [5]. This study was approved by the ethics committee of The University of Tokyo. Informed consent was obtained from each subject before the experiment.

Apparatus and procedure: In an electrically shielded room, the subject wore earplugs and a gender-matched experimenter sat facing the subject across a table on which the response devices for each were placed (Fig. 1). A screen separated the experimenter and the subject, so that the subjects could not see the experimenter's face or body, only their forearm and hand. A button was mounted on each response device, and the experimenter's box also had two red LEDs oriented along the sagittal plane of the participant. The experimenter rested his or her left or right index finger on the response key. The subject was instructed to respond using the index finger of the hand opposite to that of the experimenter, in a mirror-like fashion.

Each subject performed the reaction time task using two different stimuli (LED or experimenter's index finger) with either the left or the right hand. In reaction to the LEDs, the subject observed two LEDs, of which only the further one from the subjects was initially lit. The response cue was a momentary alternation (100 ms duration) of the LEDs, which resulted in an apparent motion of the lights with a 3–7 s interstimulus interval (ISI, 5 s on average). In the reaction to finger motion, the experimenter pressed a key as the cue for the subject's response. A visual metronome and a sheet listing a sequence of randomized ISI, which matched with the LED condition, were placed in front of the experimenter to guide the cueing so that it was not affected by the subjects' motion. The subjects performed 80 trials for each of the four conditions (i.e. two stimulus types \times two response hands) in a block design and the block order was counter-balanced across subjects.

EEG recording: The electroencephalogram (EEG) was recorded from 65 electrodes with a Geodesic sensor net [6] sampled at 250 Hz with a 0.01–100 Hz band-pass filter. All of the recordings were initially referenced to the vertex and later digitally re-referenced to the average reference. In the off-line analysis, a 0.1–30 Hz band-pass filter was reapplied. Data were segmented into 800 ms bins, including a 200 ms pre-stimulus baseline period, based on time markers for the stimulus onset. Only segments that satisfied the criteria for both task performance (those trials with a reaction time > 100 ms and within 1 s.d. for each subject) and artifact rejection (no voltage exceeding ± 80 μ V in any channel) were analyzed and baseline-corrected.

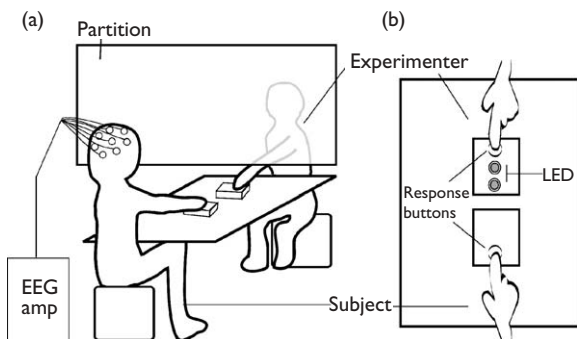


Fig. 1. Experimental setup (a) and the configuration of the stimulus–response devices (b), illustrating the case where the subject reacts with the right hand.

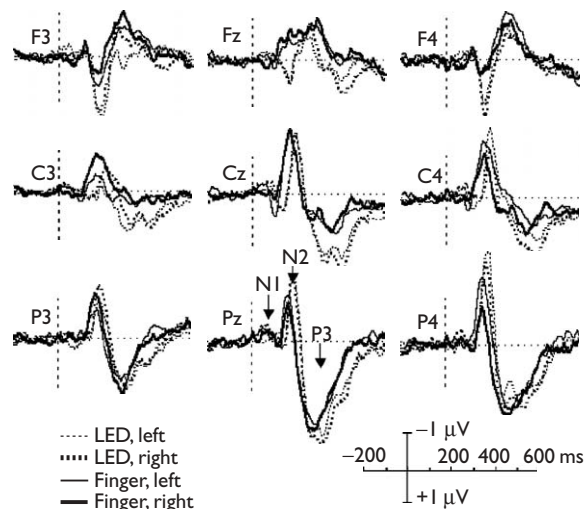


Fig. 2. Grand-averaged waveforms across the 12 subjects in response to the LEDs (dashed lines) and finger motions (solid lines) with either the left (thin lines) or right (bold lines) hand, at representative nine electrode sites. The polarity of the waveforms is plotted with negative values upward. Main ERP features N1, N2 and P3 are marked in the waveform of Pz for orientation.

ERP analysis: In this time course analysis, we did not compare the ERP latencies because when the onset timing of the cueing involves a human, it cannot be controlled precisely. Instead, we examined different neural pathways for the stimulus types, independent of the ERP latencies, using an analysis of the topographic transitions. First, as a common landmark of the neural dynamics across conditions, we determined the ERP components that were prominent across the conditions (termed N1, N2, and P3; see Fig. 2) from the group grand average waveforms. Subsequently, five 20 ms time bins, which consisted of the three peaks in the ERP components (N1, N2, and P3), and the two periods between the peaks (N1–N2 and N2–P3), were determined for each condition (the latencies of each window are shown in Fig. 3). In order to increase the S/N ratio and also to minimize the possibility of Type I errors due to a large number of electrodes [7], 63 scalp electrodes were collapsed by spatial averaging into six groups per hemisphere, so that they sparsely covered the whole of the surface (the centers of each of the sites were F3/4, C3/4, T7/8, P3/4, P7/8 and O1/2, according to the International 10–20 system). Mean amplitudes of each time bin from each subject were tested using a repeated-measures ANOVA for three factors: stimulus type (LED/finger), electrode (6 sites above), and hemisphere (left/right of the sites) in each response hand separately.

RESULTS

Behavioral measurement (reaction time): The average (\pm s.d.) reaction time in each condition was (for each response hand) 293 ± 52 ms (left) and 290 ± 65 ms (right) in reaction to the LED and 298 ± 67 ms (left) and 297 ± 77 ms (right) in reaction to finger motion. These reaction times were assessed using a repeated-measures ANOVA with the factors being stimulus type (LED/finger) and response hand (left/right); no significant main effects or interaction were detected.

ERP topographic transition: The time courses of the ERP topographies elicited in common across conditions (Fig. 3)

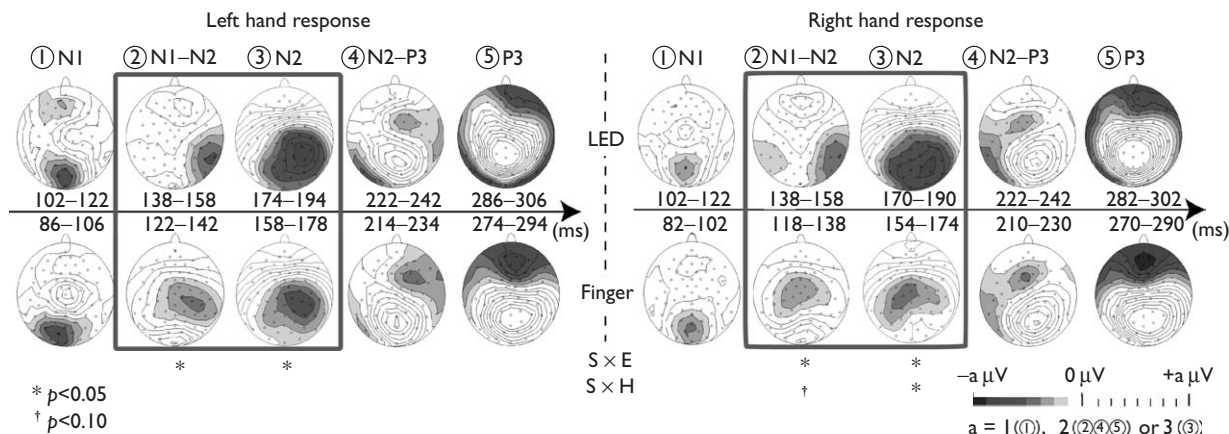


Fig. 3. Transition of the surface potential distribution illustrated as a succession of the average topography within each time window (for the definition of the time windows, see the text). The heads are viewed from the top with the noses pointing upward. Topographic differences between stimulus types (LED/finger) were compared in each time bin for the left and right hands separately, and the bins with a significant difference (in which 3-way ANOVA found an interaction between stimulus type (S) and electrode (E) or hemisphere (H)) are boxed. Note that the voltage range varied across time windows and that negative variation is gray-scaled to improve legibility.

were roughly as follows: after the visually evoked N1 around the occipital area, N2 developed with the stimulus-dependent distribution described below. Consequently, N2 was overlaid by the developing P3 component in the parietal region, which remained around the pre-central region contralateral to the response hand.

To assess the effect of stimulus type on the ERP topography, we focused on the effect of the interaction between the stimulus type and the other spatial factors (electrode or hemisphere). In both of the response hands, significant interactions, including stimulus type, were revealed in two consecutive time bins: the period between N1 and N2 (N1-N2) and the N2 peak (N2, see Fig. 3). Significant stimulus type \times electrode interactions were found in both the left hand reaction (N1-N2: $F(5,7)=4.383$, $p=0.040$; N2: $F(5,7)=5.709$, $p=0.021$) and the right hand reaction (N1-N2: $F(5,7)=6.608$, $p=0.014$; N2: $F(5,7)=3.999$, $p=0.049$), reflecting the fact that N2 was generated more anteriorly in the imitative reaction, irrespective of the response hand. Further, there were also time bins with marginally or actually significant interactions of stimulus type \times hemisphere (N1-N2: $F(1,11)=3.618$, $p=0.084$; N2: $F(1,11)=6.952$, $p=0.023$) in the right hand reaction, but not in the left hand reaction, indicating differences in the hemispheric lateralization between the two stimulus types: N2 in the imitative reaction was lateralized contralaterally to the response hand, whereas in the reaction to the LEDs, N2 was generated in the right hemisphere, irrespective of the response hand. In the other time bins, no effects involving stimulus type were found for either response hand.

DISCUSSION

This study compared the ERP responses to a simple reaction time task with two different visual motion stimuli (the apparent motion of LED lights or the finger motion of a person pressing a button) to clarify the specific neural dynamics of the imitative reaction. The time course analysis revealed clear differences in the surface topography in the developing and peak periods of the N2 component (Fig. 3). To interpret the results, the imitation-related generation of N2 was considered in both spatial and temporal aspects,

that is, in which part of the brain and in which stage of the visuomotor transfer the distinctive response took place.

As for the spatial feature of the ERP, the topography inherent in the imitative reaction can be described as follows. First, the N2 component was generated more anteriorly than in the reaction to the LEDs, as indicated by the significant interaction between stimulus type and electrode site. Second, N2 developed dominantly in the hemisphere contralateral to the response hand, while the LED-cueing elicited N2 mainly in the right hemisphere, irrespective of the response hand. Consequently, an interaction between the stimulus type and the hemisphere was evident only for the right-hand reaction (Fig. 3). These patterns indicated that the imitative neural activity was highly sensitive to the execution hand. Furthermore, although the exact location of the elicited response cannot be discussed based only on the raw-ERP, the topography in the imitative condition described above may reflect the activities of the motor areas contralateral to the response hand. This interpretation is in line with the knowledge of the mirror neuron system, that is, evidence from several studies has indicated that observing some human actions activate the observer's primary motor [1,8] or premotor [9-11] areas.

For considering the temporal aspect of processing, the distinctive period inherent to the imitation was revealed: the time window was selectively observed in the N2 component, at about 120-200 ms post-stimulus in both hands. Therefore we have to consider which process in the visuomotor transfer the time window of the N2 reflects. Previous ERP studies have indicated that the negative component with the latency discussed here in visuomotor tasks contains a motion-evoked visual potential [12,13] and premovement negativity [14,15], thus the component should reflect both the visual and motor processing [16]. However, based on the following facts and knowledge, we interpret that the distinction itself was caused by a difference in the visual, rather than the motor processing. First, the variable in the present experiment was the type of stimulus and the way in which the reaction was set invariable among conditions. Second, no differences in the reaction times among stimulus conditions were observed in the current setup. Thirdly, there are several ERP studies showing that visual responses in the anterior regions are evoked in rather

early latency, comparable to the present result. Thorpe *et al.* [17] and other studies by the same authors have revealed that the onset of visual categorization occurs less than 150 ms after stimulus, as reflected in the voltage shift over anterior electrode sites. Thut *et al.* [16] showed that the visual responses separated from motor potentials were observed over the primary motor areas at 133–145 ms. The evidence outlined above [16,17] supports the notion that the distinctive period here reflects the difference in the visual response between stimulus conditions.

In respect to the behavioral result, this was inconsistent with that of Tessari *et al.* [4]: their reaction time was significantly shorter in the imitative reaction whereas no difference was found in our result, although the present paradigm was based on theirs. This lack of agreement was probably due to the different experimental setups. We modified mainly two of their experimental conditions; the response devices were separated into ones for the experimenter and the subject (while in their study the participants shared a single response device on which two response buttons were mounted), and earplugs were used by our subjects (a point not mentioned in their paper). In fact our preliminary study replicated their setup and the reaction time results of Tessari *et al.*; however, our subjects reported that the experimenter's cueing produced slight vibrations and sounds inevitably perceived through the response device, so that the response to the finger motion required less demand than that to the LEDs. Taken together, the fact that our modified setup in the actual session revealed no reaction time-difference suggests that the reaction times in our preliminary study, and presumably those in Tessari *et al.* as well, were affected by the audiotactile information generated by the actor's button pressing.

In summary, in consideration that both distribution and latency differentiated in ERPs, we postulated that the specific topography in imitation reflected the visual response, presumably in the motor or premotor areas. Simultaneously, no conditional difference was found in the reaction times. Therefore, the results suggest that early activities of the motor-related areas induced by the observation of a matching motion do not necessarily lead to motor facilitation, at least in the sense of temporal acceleration. This interpretation is somewhat in contrast with recent evidence that has suggested that imitative actions are more facilitated than general visually guided motions; for example, observing a human movement primes the observer's identical movement [18], while no effect appears when the targets are the motions of mechanical devices [19,20]. In regard to this point, we have to consider that the current task was a simple reaction time task where the type of response was constant, so the observed action (the experimenter's cueing) worked just as a trigger of fixed and prepared motor commands. To confirm the relationships between neural and behavioral indices in motor imitation, further examinations will be needed with tasks that require 'online' visuomotor executions guided by an observed motion among several possible motor repertoires. Finally, this is one of the first observations of an ERP pattern in an imitative task, and shows the potential of this methodology for examining neural dynamics in the real-time social interactions.

CONCLUSION

This ERP study suggested that the neural pathways that are characteristic to imitative visuomotor tasks take place selectively in the stage of visual processing, at least in a simple and non-selective reaction task like that of the current study. Furthermore, it was also suggested that responses in the motor areas induced by observing a human motion can be visual rather than motor responses, and they do not necessarily lead to a facilitation of matched motor execution.

REFERENCES

1. Hari R, Forss N, Avikainen S, Kirveskari E, Salenius S and Rizzolatti G. Activation of human primary motor cortex during action observation: a neuromagnetic study. *Proc Natl Acad Sci USA* 1998; **95**: 15061–15065.
2. Muthukumaraswamy SD and Johnson BW. Changes in rolandic mu rhythm during observation of a precision grip. *Psychophysiology* 2004; **41**:152–156.
3. Nishitani N and Hari R. Temporal dynamics of cortical representation for action. *Proc Natl Acad Sci USA* 2000; **97**:913–918.
4. Tessari A, Rumiati RI and Haggard P. Imitation without awareness. *Neuroreport* 2002; **13**:2531–2535.
5. Oldfield RC. The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia* 1971; **9**:97–113.
6. Tucker DM. Spatial sampling of head electrical fields: the geodesic sensor net. *Electroencephalogr Clin Neurophysiol* 1993; **87**:154–163.
7. Oken BS and Chiappa KH. Statistical issues concerning computerized analysis of brainwave topography. *Ann Neurol* 1986; **19**:493–497.
8. Fadiga L, Fogassi L, Pavesi G and Rizzolatti G. Motor facilitation during action observation: a magnetic stimulation study. *J Neurophysiol* 1995; **73**:2608–2611.
9. Iacoboni M, Woods RP, Brass M, Bekkering H, Mazziotta JC and Rizzolatti G. Cortical mechanisms of human imitation. *Science* 1999; **286**:2526–2528.
10. Rizzolatti G, Fogassi L and Gallese V. Neurophysiological mechanisms underlying the understanding and imitation of action. *Nature Rev Neurosci* 2001; **2**:661–670.
11. Koski L, Wohlschlagel A, Bekkering H, Woods RP, Dubeau MC, Mazziotta JC and Iacoboni M. Modulation of motor and premotor activity during imitation of target-directed actions. *Cerebr Cortex* 2002; **12**:847–855.
12. Kubova Z, Kuba M, Spekreijse H and Blakemore C. Contrast dependence of motion-onset and pattern-reversal evoked potentials. *Vis Res* 1995; **35**:197–205.
13. Niedeggen M and Wist ER. Characteristics of visual evoked potentials generated by motion coherence onset. *Cogn Brain Res* 1999; **8**:95–105.
14. Arezzo J and Vaughan HG Jr. Intracortical sources and surface topography of the motor potential and somatosensory evoked potential in the monkey. *Prog Brain Res* 1980; **54**:77–83.
15. Brunia CH and van Boxtel GJ. Wait and see. *Int J Psychophysiol* 2001; **43**:59–75.
16. Thut G, Hauert CA, Blanke O, Morand S, Seeck M, Gonzalez SL *et al.* Visually induced activity in human frontal motor areas during simple visuomotor performance. *Neuroreport* 2000; **11**:2843–2848.
17. Thorpe S, Fize D and Marlot C. Speed of processing in the human visual system. *Nature* 1996; **381**:520–522.
18. Brass M, Bekkering H and Prinz W. Movement observation affects movement execution in a simple response task. *Acta Psychol (Amst)* 2001; **106**:3–22.
19. Castiello U. Understanding other people's actions: intention and attention. *J Exp Psychol Hum Percept Perf* 2003; **29**:416–430.
20. Kilner JM, Paulignan Y and Blakemore SJ. An interference effect of observed biological movement on action. *Curr Biol* 2003; **13**:522–525.

Acknowledgements: We thank Dr S. Shimada, A. Senju and M. Miyazaki for their contribution to this work. This study was supported by a Grant-in-Aid for Scientific Research from the Ministry of Education, Culture, Sports, Science and Technology, Japan (No. 30323455). It was also partly supported by the Center for Evolutionary Cognitive Science at the University of Tokyo.