

Neural substrates involved in imitating finger configurations: an fMRI study

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Imitation plays a very important role in human cognition. Because previous neuroimaging studies on human imitation used rather simple actions as target stimuli, some aspects of imitation such as perceiving target actions or manipulating one's own mental image could not be studied. We used complicated non-symbolic (S-) and symbolic (S+) finger configurations as target stimuli in order to study the neural

substrates involved in the perception of target actions and mental image manipulation during imitation. Bilateral supramarginal gyrus activation was detected when the S- condition was compared with the S+ condition. Our result suggests the involvement of the supramarginal gyrus especially for the imitation of novel actions. *NeuroReport* 12:1171-1174 © 2001 Lippincott Williams & Wilkins.

Key words: Finger configuration; Ideomotor apraxia; Imitation; Mental image; Supramarginal gyrus

INTRODUCTION

Imitation is thought to play a critical role in human learning or communication [1,2]. The process of imitating other people's actions contains complex cognitive elements such as visual perception of target actions, transforming perceived actions into one's own body and/or motor representation, and simulation of one's own motor image [3-5]. We used fMRI to study the neural substrates involved in imitating finger configuration.

Left inferior parietal lesions are known to cause ideomotor apraxia (IMA), a pathological state exhibiting deficits in pantomiming on verbal command or gesture imitation. To explain ideomotor apraxia, Heilman *et al.* proposed that the motor engrams for skilled movements are stored in the left supramarginal gyrus and damage to this area leads to IMA [3]. On the other hand, Goldenberg *et al.* suggested that IMA is derived from the poor perception of target postures [5]. In neuroimaging studies, imitation has become an important topic since the report of mirror neurons in monkeys [6], but few studies on the cerebral activity during real imitation actions of human subjects have been performed. Iacoboni *et al.* and Krams *et al.* performed studies on human imitation that included the subject's real action during data acquisition [7,8]. The stimuli used in both of the studies were very simple; the subjects were required to raise their fingertips slightly according to the presentation of line-drawn fingers or finger pictures. In both studies various brain activations were reported, including in the parietal area. However, the stimuli were too simple to include some elements of imitation such as the detailed analysis and perception of

target posture, transformation from perceived posture into one's own body image or manipulation of the motor image to produce real action. In order to study those elements in action imitation, we performed an fMRI study using rather complicated stimuli, i.e. finger configurations with or without symbolic meaning.

MATERIALS AND METHODS

Subjects: A total of nine graduate students (six male; mean age 25.2 years; range 22-34) participated as normal volunteers. All subjects were fit, healthy, on no medication, and free from any history of neurological or psychiatric illness. All of them gave written informed consent. They were all strongly right-handed on the Edinburgh Handedness Inventory [9].

Tasks: An imitation task with three conditions was used. In the first (S-) condition, 10 pictures of meaningless (in Japanese culture) finger configurations were presented to the subjects (three such items are shown in Fig. 1a). The subjects were required to imitate the finger configuration using their right hand, during the stimulus presentation. Stimuli were presented for 2 s each (SOA = 3 s, ISI = 1 s, 10 pictures in random order per block, block duration = 30 s). The second (S+) condition was a control condition: pictures of finger configurations (Fig. 1b) with symbolic meaning were presented in a manner identical with that of the S- condition. The third condition was a rest condition: a fixation point was shown instead of finger pictures with the same SOA and ISI. Subjects were instructed just to watch it. The three conditions were repeated four times in

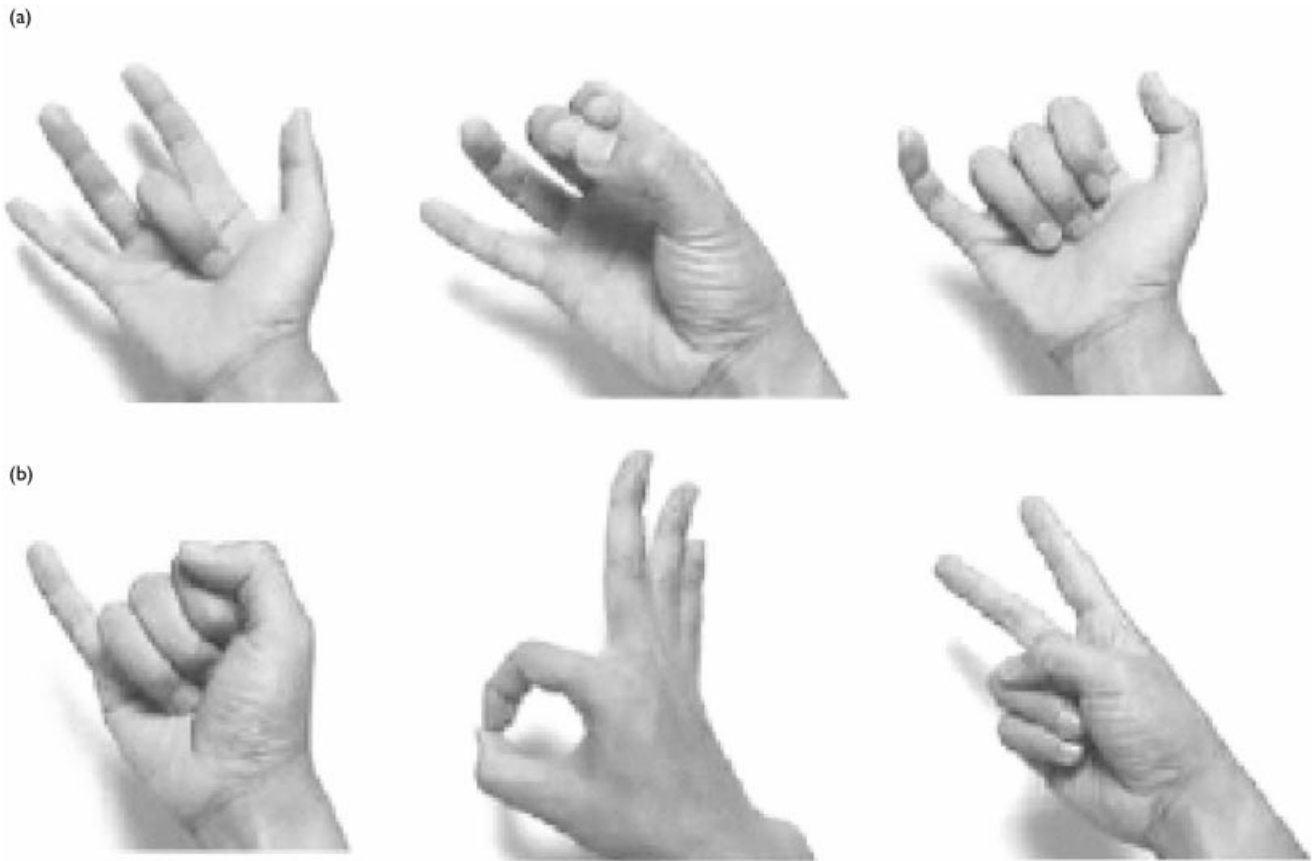


Fig. 1. Examples of visual stimuli. (a) Examples of finger configuration without symbolic meaning (S⁻, top row), (b) with symbolic meaning (S⁺, in bottom row). Three of the ten pictures are shown for each condition. In (b) the usual meanings of the configurations are promise, OK, and scissors from left to right.

a counter-balanced order such as, rest: S⁻; S⁺; rest, S⁺; S⁻; rest, S⁺; S⁻; rest, S⁻; S⁺. The visual stimuli were controlled by a personal computer. They were projected onto a screen by a liquid crystal display projector seen through a mirror set above their eyes as the subjects lay in the MRI machine. The visual angle was $5.3 \times 5.3^\circ$. The subjects' performance was monitored through the window at the MRI control console. All responses were estimated as correct or incorrect and recorded into the list of the stimuli for each subject. Responses were estimated as correct whenever fingers to be extended and those to be folded were correct.

fMRI: A conventional 1.5T MRI scanner was used (GE, Signa). A total of 72 scans were acquired with a gradient echo EPI sequence (TR/TE = 5000/40 ms, FA = 90° , FOV = 220 mm, matrix = 64×64 , 32 axial slices, 5 mm slice thickness without gap). The first four scans were removed to avoid initial instability. Data analysis was performed using SPM 96 [10]. All EPI images were spatially normalized with MNI template for group analysis. Imaging data were corrected for head movements and signal intensity variation and smoothed with an isotropic Gaussian kernel 10 mm FWHM. Significance was assessed using the delayed box-car reference.

RESULTS

The mean number of incorrect responses was 3.4 (range 2–5) among 80 responses. All incorrect responses were made in the S⁻ condition and most of them were within the first S⁻ block. Most of the incorrect responses were a timeout type (subjects failed to make any response or made uncertain finger movement and skipped to the next one). This result was consistent with the subjects' comments after the experiment that it was an effortful task for them to imitate meaningless finger configurations without seeing their own hand, even though it had been confirmed that they could imitate all stimuli in both the S⁻ and S⁺ conditions promptly and completely in front of a PC monitor outside the MRI room.

For fMRI data analysis, the thresholds for activation were set at $p < 0.001$ for voxel level. In Fig. 2a (S⁻ vs rest) and Fig. 2b (S⁺ vs rest), activation which was corrected for multiple comparison at the extent threshold of $p < 0.05$ is shown. In S⁻ vs rest, there was activation in the right SMG (Fig. 2a) which was not observed in S⁺ vs rest. The result of the comparison between S⁻ and S⁺ is shown in Fig. 2c (S⁻ vs S⁺; uncorrected for multiple comparison). Activated areas are listed in the order from high to low Z score in Table 1. In the comparison S⁻ vs S⁺, only bilateral parietal activation was significant. No significant activation was

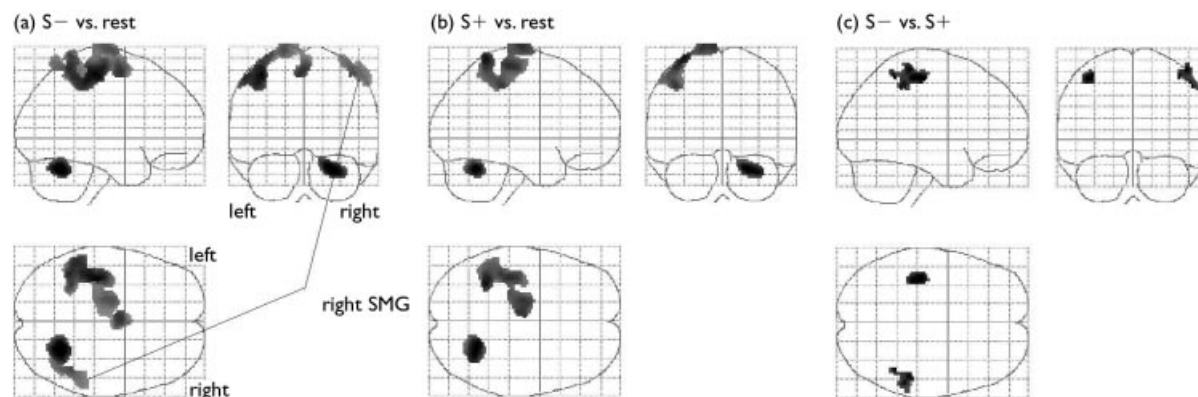


Fig. 2. The results of the comparison among three conditions shown in a transparent brain system. (a) S- vs rest, (b) S+ vs rest, (c) S- vs S+. The significance level was $p < 0.001$ at the voxel level.

Table I. Significant activation detected in the comparison of the three conditions, S- vs rest, S+ vs rest and S- vs S+.

Area	Left/right	Brodmann area	Coordinates of peak voxel			Z score
			x	y	z	
S- vs rest						
Cerebellum	R		25	-56	-13	7.30
MI	L	4	-37	-19	51	6.79
SMG	L	40	-41	-41	57	6.07
SMA	L	6	-2	1	51	5.81
SI	L	2	-33	-39	67	5.41
PM	L	6	-18	-4	68	4.95
MI	L	4	-29	-20	67	3.59
SMG	R	40	43	-42	53	4.95
S+ vs rest						
SI	L	2	-29	-39	67	6.85
Cerebellum	R		22	-54	-13	6.39
SMA	L	6	-2	3	51	5.53
MI	L	4	-37	-20	58	5.35
SMA	L	6	-6	-8	72	5.10
PM	L	6	-16	-4	68	5.08
SMG	L	40	-39	-28	44	4.66
MI	L	4	-25	-19	68	4.20
S- vs S+						
MI/SI/SMG	L	4/2/40	-35	-25	52	3.40
			-37	-16	49	3.27
SMG	R	40	49	-26	57	3.31
			41	-40	53	3.10

L, left; MI, primary motor area; PM, premotor area; R, right; SI, primary sensory area; SMA, supplementary motor area; SMG, supramarginal gyrus.

detected in the comparison of S+ vs S-. In both of the comparisons between S- and rest or between S+ and rest, strong right cerebellum activation was observed.

DISCUSSION

In the comparison of S- vs S+ conditions, significant activation in the bilateral SMG was observed. In comparison with the rest condition, both S- and S+ conditions showed activation in the left SMG, but only the S-

condition showed activation in the right SMG. According to interviews after the experiment, subjects did not have to carefully analyze the position of each finger in the S+ condition, because they were well accustomed to the stimuli. Contrarily the S- condition required more detailed visual analysis of the target stimuli as well as somesthetic analysis/integration than the S+ condition. Iacoboni *et al.* also suspected that activation in the right SMG in their fMRI study of finger imitation might imply that the

perceived information of the observed action, such as the angle of a finger joint, is stored in this area [7]. Goldenberg *et al.* studied the imitation task of finger postures and the imitation task of hand postures in patients with left or right brain damage [11]. They reported that the right brain damaged patients performed poorly in the finger task compared with the hand task, and their performance in the finger task was poorer than that of the left brain damaged patients. They supposed that the finger posture imitation task contained larger requirements for the perception of target postures and this function might be involved more in the right hemisphere than in the left. Consequently, we suppose the right SMG activation detected in S- vs S+ conditions in our study might be related to the perception of target actions of the S- condition that required more careful visual analysis than in the S+ condition.

The subjects had to feel their own fingers because they could not see them during the tasks especially imitating unaccustomed finger configurations in S- condition. The activation in the left primary motor and sensory areas in the comparison of S- vs S+ might be related to this effort. The sensory and/or motor representation of fingers might be necessary for the manipulation of mental representations required in the S- condition. The left SMG activation in the comparison S- vs S+ might show the deep involvement of this area in preparing and executing novel finger configurations which require integrating several simple actions (each finger posture) into a more complex one. Lesions in the inferior parietal lobule are known to cause disturbances in complex polymodal integration of somesthetic and visual representation such as ideomotor apraxia [3,4,11]. Our result is consistent with these neuropsychological findings.

CONCLUSION

An fMRI study on finger configuration imitation was performed in order to study the neural substrates involved in action imitation. We used novel complex finger configurations without symbolic meaning, as well as those with symbolic meaning, in order to study the elements of action imitation such as visual analysis of target action or manipulation of mental representations. Compared with the S+ condition, bilateral SMG activation was observed in the S- condition. Analyzing the cognitive process of imitation and considering the neuropsychological findings on imitation deficits, the right SMG activation is thought to be related to the perception of target postures. The left SMG activation might be involved in preparing to execute novel finger configurations, which necessarily includes the process of integration of complex actions from simple ones.

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