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3 Imitation Induced Deactivation in the Brain: A PET Study

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Abstract

We presented many trial-unique, relatively new, meaningless hand-finger actions without goals to observers to observe and to imitate during PET scanning. These actions were not trained before the experiment. The main results were that deactivation in the prefrontal cortex was observed during imitation of hand-finger actions compared with the observation and the rest conditions. These results were discussed in relation to the problems of the

self and the other in which the prefrontal cortex is involved. No activation was observed in Broca's area during observation and imitation of actions employed in the present experiment. A large number of trial-unique, new actions without goals may be responsible for the absence of activation in Broca's area.

Introduction

Disorders of actions, including imitation, are called apraxia. There are a variety of tests of imitation for apraxic patients: Actions to be imitated are transitive or intransitive actions, limb or buccofacial actions, meaningful or meaningless actions, actions directed to personal space (the self body) or to extrapersonal space, single or sequential actions, automatic or intentional actions, and so on. Apraxic patients imitate some actions easily, but they have difficulty in imitation of other actions (e.g., Heilman & Rothi, 2003). Thus, imitation is not a single phenomenon. There may be another aspect of the diversity in imitation in experiments with normal subjects. An observer may imitate actions with goals or without goals. An observer may imitate well-known, over-trained one or two actions in some situations. But in other situations she/he may imitate many relatively novel actions. Other diversity is that in some situations, an observer considers the mind of a model, but in other situations an observer just mimics the external appearance of model's action. The former case is the problem of the 'theory of mind' or of mind reading (Gallese & Goldman, 1998). Thus, imitation is not a single entity.

The discovery of mirror neurons in the monkey ventral premotor cortex (F5 area, it is homologous to Broca's area, Gallese et al. 1996) facilitates the functional brain imaging studies of imitation and its relation to Broca's area. The mirror neuron system has expanded to cover social cognition, that is, simulation of other's mind in mind reading (Gallese & Goldman, 1998). However, it is not common for Broca's area to be active in mind reading. Rather, the medial part of the prefrontal cortex is activated in mind leading or the 'theory of mind' situations (e.g., Fletcher et al., 1995). The midline structures, including the medial part of the prefrontal cortex, become active when we pay attention to the inside of our and of others' mind (e.g., Damasio, 1999; Decety and Sommerville, 2003; Northoff & Bermpohl, 2004; Amodio

& Frith, 2006). When we pay attention to the external visual world, the medial prefrontal cortex is often deactivated (Shulman et al., 1997; Gusnard & Raichle, 2001).

In the present study, we presented many meaningless hand-finger actions (for short, hand) without goals to participants to observe and to imitate during PET scanning. These actions were not trained before the experiment and participants imitated these actions during the experiment. Compared with previous studies with small number of actions, different activation pattern might be expected in the present experiment. It was not necessary for participants to consider model's mind in this experiment. *Deactivation* rather than activation might be expected in the medial prefrontal region during imitation, for participants just mimiced the external appearance of model's actions and did not pay attention to the internal mind of the model.

1. Method

1.1. Participants

Participants were 8 male right-handed graduate and undergraduate students. A written informed consent was obtained from each participant using forms approved by the ethical committee of National Institute for Longevity Sciences and the declaration of Helsinki (1991). All of the participants were healthy, with no past history of psychiatric or neurological illness, and were not receiving any medication.

1.2. Behavioral procedures

Hand-finger actions without a goal were employed. There were twenty-eight actions and each action was presented on a goggle screen. Each action was presented for 1 s and repeated for three times in a trial. After the three presentations, the next action was presented with 1-s interstimulus interval. Thus, these actions were trial-unique.

There were three conditions: observation, imitation and rest. In the observation condition, participants observed an action repeated for three times presented on the goggle. In the imitation condition, participants observed the first presentation of the action then executed or imitated the same action for two times in line with that on the goggle. In the rest condition, participants closed the eyes and lay down quietly. Only a single action condition was presented in a block of PET scanning. The order of the presentation of these conditions was different between participants.

1.3. PET scan

Each participant was positioned in a PET scanner (Siemens/CTI ECAT EXACT HR). The room was darkened and kept quiet during the experiments. Prior to the PET measurements, a transmission scan was performed three rotating $^{68}Ge/^{68}Ga$ sources. The emission scan was started immediately after the administration of a bolus injection of approximately 15 mCi (555MBq) $H^{15}{}_{2}O$ using the three-dimensional (3D) collection mode. All injections were performed in a single scanning session for each participant. Attenuation-corrected data were reconstructed into 63-image planes with a resolution of 6 mm at full-width at half-maximum.

1.4. PET analysis

Preprocessing procedures and statistical analysis of PET images were performed using Statistical parametric mapping software (SPM2, Wellcome Department of Cognitive Neurology, London). After the head-motion correction, all the PET images were normalized to the MNI PET template brain for each subject, and smoothed using a Gaussian kernel of 16mm-FWHM. Each preprocessed image was normalized to the mean regional cerebral blood flow (rCBF) of 50 ml/dl/min. A two-way (7 tasks x 8 subjects) ANOVA was implemented in the general linear model at each voxel to estimate the task effect on cortical activation. To test the differential task effects between the imitation and observation tasks in each action type, t statistics were applied at each voxel using linear contrasts of parameter estimates. The resulting set of voxel values for each contrast constitutes a statistical parametric map of the t statistic, SPM{t} (Friston et al., 1995). Activation was thresholded at $p<0.001$ for the height, and corrected to $p<0.05$ for multiple comparisons using the cluster size.

Table 1. Coordinates and t-values for regions of significantly higher activation in the main effect of imitation compared with observation

Foci of activation	Coorinates *x*	*y*	*z*	t-value	cluster size (voxels, 2x2x2mm)
L. precentral/postcentral gyrus (M1/SI)	−38	−30	66	8.51	3789
L. medial frontal gyrus (SMA)	−4	−8	52	4.34	part of same cluster
R. cerebellum	32	−50	−30	8.09	13788
	16	−60	−20	8.07	part of same cluster
L. cerebellum	−34	−52	−32	7.27	part of same cluster

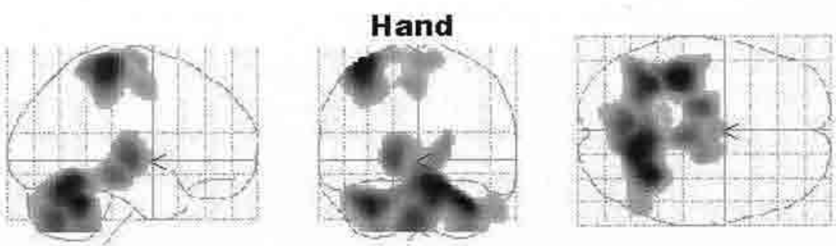

Figure 1. Main effect of imitation vs. observation of each condition.

2. Results

2.1. Imitation vs observation

When activation to observation was subtracted from that to imitation, activation in movement-related areas was observed (see Table 1 and Figure 1). The left precentral/postcentral gyrus, the supplementary motor area, the bilateral cerebellum were active.

2.2. Observation vs imitation

In this comparison, activation was observed in the frontal cortex bilaterally (the medial frontal gyrus, the frontal pole) in the hand-finger action condition. In other words, deactivation was observed in the imitation compared with the observation condition in these regions (see Table 2 and Figure 2). The right superior temporal sulcus (STS) and the left middle temporal gyrus (MTG) were also active. Activation was observed in the left angular/temporopapietal junction (AG/TPJ) and the right rhinal gyrus. As presented below, the

Table 2. Coordinates and t-values for regions of significantly higher activation in the main effect of observation compared with imitation

Foci of activation	Coorinates x	y	z	t-value	cluser size (boxels, 2x2x2mm)
R. rhinal gyrus	34	−8	−30	5.59	2293
R. superior temporal sulcus	60	−10	−10	5.23	part of same cluster
L. angular gyrus/temporoparietal junctio	−42	−64	26	5.49	630
R. medial frontal gyrus (dorsomedial pref	12	42	50	4.77	2797
L. frontal pole	−12	70	14	4.48	part of same cluster
L. medial frontal gyrus (dorsomedial pref	−8	30	50	4.29	part of same cluster
R. frontal pole	20	66	14	4.17	part of same cluster
R. medial frontal gyrus (ventromedial pre	4	54	−8	3.85	part of same cluster
L. middle temporal gyrus	−54	−14	−22	4.52	870

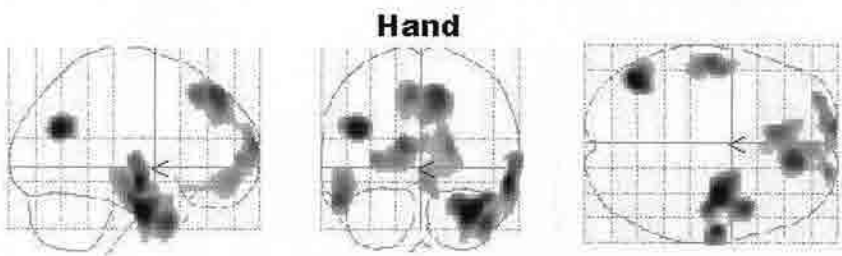

Figure 2. Main effect of observation vs. imitation of each condition.

imitation-induced deactivation was observed compared with the rest condition.

2.3. Activation in Broca's area

No activation was observed in Broca's area and the right homologous area (the posterior part of the inferior frontal gyrus) in any comparisons between the experimental conditions and in comparison these conditions with the rest condition.

3. Discussion

3.1. Imitation-induced deactivation in the prefrontal cortex

The main results of the present experiment were the widespread deactivation in the prefrontal cortex found in the imitation conditions. The deactivation was observed during imitation of hand-finger actions. Deactivation in the frontal cortex was observed in many cognitive tasks (e.g., Mckiernan et al., 2003; Shulman et al., 1997). Among them, the most important is the problem of the self and the other, because imitation is related to other's actions (Gusnard & Raichle, 2001). The mirror neuron system expanded to cover the problem of the self and the other (theory of mind and mind reading; Gallese & Goldman, 1998). It is well known that the midline structures including the medial prefrontal cortex are active when we pay attention to the mind of the self and the other, that is, retrieval of autobiographical memory, evaluation of the self and theory of mind (e.g., Fletcher et al., 1995; Maguire & Mummery, 1999; Zysset et al., 2002). When we pay attention to the external aspects of the self and the other, for example, the body ownership and the agency of actions (authorship) and imitation, the lateral parts of the brain were activated (e.g., Farrer & Frith, 2002). Furthermore, when we pay attention to the external visual world, the midline structures are *deactivated* (Gusnard & Raichle, 2001).

Activation or deactivation of the midline structures may occur depending on task requirements. In the present experiment, the participants were not necessary to consider the mind of the model. They pay attention to the external appearance of actions performed by the model. In this situation, the initiative was in the side of the model (the other), not in the self. It may be necessary for the participants to inhibit the selves to imitate model's actions.

There are two kinds of deficits in imitation: difficulty in imitation and excess of imitation. The latter is important in the present context. Lhermitte (1986) and Lhermitte et al. (1986) proposed the concept of the 'environmental dependency' in patients with lesions in the frontal cortex. Patients with the environmental dependency use and manipulate objects compulsively and imitate others' behaviors obsessively (see also De Renzi et al., 1996; Brass et al., 2003). These patients are often dementia (Shimomura & Mori, 1998). As pointed out by Meltzoff (1988), humans are *Homo imitans*. Only humans have evolved an ability to easily imitate others' actions. Humans often have to inhibit this innate imitation tendency. Thus, the self and the environment are confronting each other. Frontal patients with dementia reduce the control over the self. This in turn strengthens the control of the environment on the self. The environmental dependency syndrome may support the present interpretation of the relation between imitation-induced deactivation and the self in imitation.

The imitation-induced deactivation in the prefrontal cortex was also observed by near infrared spectroscopy (NIRS, unpublished observation by the first author).

3.2. Absence of activation in Broca's area

Contrary to many previous experiments of action observation, imitation or execution (e.g., Rizzolatti et al., 1996; Grafton et al., 1996; Binkofski et al., 1999; Iacoboni et al., 1999; Nishitani & Hari, 2000; Buccino et al., 2001; Koski et al., 2002; Nishitani & Hari, 2002; Grezes et al., 2003; Hamzei et al., 2003; Johnson –Frey et al., 2003; Leslie et al., 2004; Rumiati et al., 2004), in the present experiment, we did not find activation in Broca's area (Brodmann's areas 44 and/or 45) in the observation and the imitation conditions compared with the rest condition. These results suggest that there may be conditions under which Broca's area is activated during observation and execution (imitation) of actions. One of the candidates is the presence of visual goals (Koski et al., 2002; Johnson-Frey et al., 2003).

Another candidate is the degree of training of to-be-imitated actions. The number of actions is also one of candidates. Many researches which found activation in Broca's area employed small number of relatively well trained actions. Thus, observers performed actions quickly and almost automatically in response to the model's actions. In this situation, model's action may simply set occasion to select and initiate one of a few predetermined actions for the observer, as Makuuchi (2005) pointed out. In the present experiment, we presented many trial-unique, relatively new actions. These factors and the factor of no visual goal may be responsible for the absence of activation in Broca's area in the present study.

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