

Motivation Modulates the Activity of the Human Mirror-Neuron System

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It is not known whether the mirror-neuron system is modulated by motivation, such as hunger. In this study, 2 groups of healthy participants underwent 2 functional magnetic resonance imaging scanning sessions separated by 1.5 h interval. During each session, participants were presented with video clips of another person grasping objects or grasping food. The first session was conducted after participants from group 1 had fasted. Then these participants were allowed to eat and were scanned again. Participants from group 2 had a meal before the first session. Food-related stimuli elicited specific hemodynamic response in the parahippocampal gyrus, orbitofrontal cortex, and amygdala, when participants were in a hungry state as compared with a satiated state. In addition, regions that belong to the mirror-neuron system, including the inferior frontal gyrus, and the posterior parietal cortex showed greater response when participants were hungry. Increased activity was also detected in the extrastriate body area. A positive correlation was observed between the self-report ratings of hunger and the hemodynamic activity in the inferior frontal gyrus as well as in the amygdala. Our results suggest that motivation to eat modulates the neural activity in the mirror-neuron system, facilitating the preparation or the intention to act.

Keywords: functional magnetic resonance imaging, hunger, mirror-neuron system, motivation, motor cognition

Introduction

An impressive range of evidence demonstrates that perceiving other people's behavior activates corresponding motor representations in the observer (e.g., Dijksterhuis and Bargh 2001). This phenomenon arises from the direct perception-action link mediated by a distributed network of neural regions in the posterior parietal, premotor cortices, and inferior frontal gyrus. Electrophysiological studies conducted in monkeys demonstrated sensory-motor neurons—also called “mirror neurons”—located in this parietofrontal circuit, that discharge both when the individual is executing a goal-directed action and when watching the same action being performed by another conspecific (for a recent review, see Rizzolatti and Craighero 2004). In humans, a similar network has been reported to be activated during both the generation of actions and the observation of actions made by other people (for a review, see Jackson and Decety 2004).

This mirror mechanism may subserve different functions, including action understanding (Rizzolatti and Craighero 2004), empathy (Preston and de Waal 2002; Gallese 2003; Meltzoff and Decety 2003; Decety and Jackson 2004; Decety and Lamm 2006), imitation (Brass and Heyes 2005; Iacoboni 2005), action prediction (Blakemore and Frith 2005), action simulation

(Wilson and Knoblich 2005), and social interaction (Sommerville and Decety 2006).

Given that the perception-action system evolved primarily in service of the survival of the organism (Sperry 1952), the idea arises that homeostasis should modulate the motor mirror-neuron system. This aspect has not yet received much attention: relatively little is known about how the mirror-neuron system is affected by motivational state. However, it is widely acknowledged that motivation impacts behavior by directing attention to select some behavior and courses of action over others. Of importance, Ferrari et al. (2005) reported a series of single-neuron recordings in monkeys addressing observation of eating behavior. Their results indicate that such an observation significantly enhanced eating behavior in the observer, even when only the sound of eating actions was played. They suggested that eating facilitation triggered by observation or listening of eating actions can rely on the mirror-neuron system of the ventral premotor cortex that provides a matching between the observed/listened action and the executed action.

In the present study, we examine the effect of physiological need on the mirror-neuron system. In particular, we investigated the effect of hunger on the neural network that mediates the perception of others' action directed toward food, such as food grasping. Food is obviously a major motivator of behavior. In any species including humans, foraging and consumption of food are critical activities involving a good deal of time and energy investment. Therefore, it was predicted that variations in hunger would selectively modulate the responses in brain regions already known to be involved in positive/appetitive stimuli (i.e., parahippocampal gyrus, fusiform gyrus, amygdala, and orbitofrontal cortex) in participants watching appetitive visual stimuli (Rolls 1996; LaBar et al. 2001; Morris and Dolan 2001). Moreover, we also anticipated greater hemodynamic signal in the mirror-neuron network, including the inferior frontal gyrus, the posterior parietal cortex, and the extrastriate body area (EBA) when participants watched grasping food.

Participants were requested to arrive at the neuroimaging laboratory in a hungry state (i.e., having abstained from food, but not water for approximately 12 h). They were scanned while watching video clips depicting a human grasping food (motivationally relevant stimuli) or objects (motivationally irrelevant stimuli). Then after having a meal, they were scanned again during a satiated state (hungry-satiated group). To control for habituation effects, a control group of participants was scanned in a satiated state both times (satiated-satiated group). Individuals from both groups spent an equivalent amount of time out of the magnet (i.e., between the 2 magnetic resonance imaging [MRI] sessions).

Material and Methods

Participants

Twenty right-handed subjects (10 females and 10 males, age ranging between 19 and 28 years) with no history of neurological or psychiatric disorders were included in the study and were compensated for their participation. Participants' body mass index was within normal (18.5–24.9) to overweight (25.0–29.9) range. Participants were instructed not to eat food for at least 12 h prior to the imaging session. To help insure that that refrained from eating, they were informed that blood sugar level would be checked upon arrival. All participants complied with the instructions and reported feeling hungry at the time of testing. The study was approved by the University Ethics Committees. Written informed consent was obtained from each participant prior to entry. Participants were not given any additional information regarding the aim of the study. All participants reported liking what has been termed "fast food" (e.g., hamburgers, hot dogs, etc.).

Stimuli

A series of short (2.5 s) digital color video clips were shown in each functional magnetic resonance imaging (fMRI) session. The stimuli were presented via a computer connected to a video projector and reflected into a mirror positioned in front of subjects' eyes. Twenty-four videos depicted a human person (male or female) grasping food (e.g., grasping a hamburger), and 24 videos depicted grasping objects (e.g., grasping a sponge). The food and object items were selected to match in terms of grasping affordances, as well as in their relative timing (reaching 1 s, grasping 0.5 s, and taking off 1 s). Static pictures of food and objects were also edited from the videos and presented for 2.5 s in the scanner. Finally, an additional stimulus category consisted of a subset of the scrambled food and object pictures that were Gaussian-blurred so that the food and the objects were not identifiable. The condition of observation of the scrambled pictures (also presented for 2.5 s) was chosen as a baseline for the other conditions (the observation of grasping food, grasping objects, food, and objects).

Procedures

Twenty participants took part in 2 fMRI sessions separated by 1.5 h interval. Before each session, participants filled out the Visual Analog Scales (VAS) (Hill and Blundell 1982), a standard scale used to assess hunger and the motivation to eat. Upon their arrival to the laboratory, participants were randomly assigned to the hungry-satiated group (5 females and 5 males) or to the satiated-satiated group (5 females and 5 males). Participants from the first group were fed a meal of their choice between the 2 fMRI sessions. Participants from the latter group were also fed a meal of their choice before the first fMRI session that started 1 h later. To ensure that participants attended to the stimuli during the scanning sessions, they were asked to report the stimulus items they had seen during scanning. In addition, different items were presented in the 2 sessions.

fMRI Acquisition

fMRI data were acquired on a 3-T head-only Siemens Magnetom Allegra System equipped with a standard quadrature head coil. Changes in blood oxygenation level-dependent (BOLD) T_2^* -weighted magnetic resonance (MR) signal were measured using a gradient echo-planar imaging (EPI) sequence (repetition time [TR] = 3 s, echo time [TE] = 30 ms, field of view [FOV] = 192 mm, flip angle = 80°, 64 × 64 matrix, 40 slices/slab, slice thickness = 3 mm, no gap, voxel size = 3.0 × 3.0 × 3.0 mm). For each scan, a total of 180 EPI volume images were acquired along the anterior and posterior commissures plane. Structural MR images were acquired with a magnetization-prepared rapid gradient-echo sequence (TR = 2500, TE = 4.38, FOV = 256 mm, flip angle = 8°, 256 × 256 matrix, 160 slices/slab, slice thickness = 1 mm, no gap). This anatomic sequence was run in each fMRI session. Head movements were minimized by using a foam pillow and padding.

Each fMRI session comprised 2 EPI runs. Each run followed a 24-s ON/3-s OFF block design with 5 conditions that included the observation of grasping food (GF), observation of grasping objects (GO), static pictures of food (PF), static pictures of objects (PO), and scrambled pictures (SP). Each block was repeated 4 times in each run and contained 8 movies of

the same category (e.g., GF) separated by 0.5 s of black screen. Two consecutive blocks were separated by a 3-s pause of black screen. The order of the blocks was randomized. The order of the 2 runs was inverted from subject to subject.

fMRI Data Preprocessing

Image processing was carried out using SPM2 (Wellcome Department of Imaging Neuroscience, London, UK), implemented in MATLAB 6.1 (Mathworks Inc., Sherborn, MA). Using standard SPM procedures, images were realigned and normalized to the Montreal Neurological Institute (MNI) standard brain. The normalized images of 2 × 2 × 2 mm were smoothed by a full-width half maximum 6 × 6 × 6 Gaussian kernel. This smoothing is necessary to fulfill the statistical assumptions of the random-effect analysis.

Random-Effect Statistical Data Analysis

Preprocessed data were analyzed subject-by-subject using the standard general linear model (GLM) approach of SPM2. Four *t*-contrast maps were calculated: GF versus SP, GO versus SP, PF versus SP, and PO versus SP (i.e., baseline) for each participant of each group (hungry-satiated and satiated-satiated) at each session (the first and second sessions). All these *t*-contrast images, 4 conditions (GF vs. SP, GO vs. SP, PF vs. SP, and PO vs. SP) × 2 groups (hungry-satiated and satiated-satiated) × 2 sessions (the first and second), comprised the data for a 3-way analysis of variance in SPM2 second-level analysis (random-effects), which allows for an appropriate nonsphericity correction for this repeated measurement design. This 2-stage analysis accounted first for intra-subject (scan-to-scan) variance and second for between-subject variance. At the group level, a voxel-by-voxel single sample *t*-test was then performed to test if the contrast significantly differed from zero. Clusters were considered significant only if they were composed of at least 5 contiguous voxels, each of which having a $P < 0.005$ (uncorrected).

Furthermore, to assess the motivational effect (i.e., hungry) on visual responses to grasping food relative to objects, we tested the specific interactions if there were significant activations during the first relative to the second session within each group as well as across 2 groups. That is, (GF-GO) hungry minus (GF-GO) satiated in the hungry-satiated group was compared with (GF-GO) satiated minus (GF-GO) satiated in the satiated-satiated group on the second-level analysis. To ensure that the brain regions in the subtraction procedures reflected positive activations to the observation of grasping food in the hungry condition and not deactivations to the observation of grasping objects in the satiated condition, we inclusively masked the contrasts (mask threshold = $P < 0.05$) by the main effect of stimulus category in the hungry state, that is, [(GF-GO) hungry - (GF-GO) satiated] inclusively masked by (GF-GO) hungry (LaBar et al. 1999, 2001). This procedure is statistically equivalent to a motivational state by stimulus category separately.

Conjunction Analyses

To identify brain regions that showed significant main effects of stimulus category irrespective of motivational state (e.g., GF-specific and GO-specific activations), we conducted separate conjunction analysis that conjoined GF versus GO and GO versus GF contrasts across 2 testing sessions within each group. Conjunction analyses have been described as a method to test if both contrasts, for example, the (GF-GO) contrasts at the hungry and satiated status, are different from zero in a particular voxel. All these analyses were performed at the second level, that is, on the contrast images obtained from the single-subject analyses and were therefore random-effect analyses.

Direct Comparisons

Once the clusters activated by the specific interaction related to the motivation effect on watching grasping food were determined as well as a priori hypotheses about the implication of the mirror-neuron system, we tested within these clusters if the activation caused by GF was significantly stronger than that determined by GO across the testing sessions. Using the toolbox MarsBar (<http://marsbar.sourceforge.net>), for 4 clusters of Table 3 and for each participant, we evaluated the GLM used for the group analysis but considered the mean BOLD signal of the voxels composing each cluster instead of the voxel-by-voxel values used

in the group analysis. This method yielded a single time series and a single set of GLM parameters for each cluster and subject. We then calculated the contrast values for (GF-GO) each subject separately across each testing session. Finally, we tested if these contrast values had a mean larger than zero using a one-sided *t*-test with degrees of freedom = 9. This analysis was a random-effect analysis for the region of interest (ROI).

Simple Regression

To elucidate if the BOLD response was dependent on the motivation status, we conducted the simple regression on the basis of each participant VAS ratings and ROI analysis. Using the toolbox MarsBar to extract the mean BOLD signal of the voxels composing each activated cluster of Table 3, simple regression analyses was performed at the second level, that is, on all the contrast values for GF obtained from the single-subject analyses and all the VAS ratings from each subject at each session.

Results

Behavior VAS

Participants from the hungry-satiated group scored 43 (standard deviation [SD] = 3) before the first fMRI session and 13 (SD = 1) before the second fMRI session. This decrease in motivation to eat was statistically significant ($P < 0.0001$). Participants from the satiated-satiated group scored 10 (SD = 1) before the first fMRI session and 12 (SD = 4) before the second fMRI session (Fig. 1). No statistical difference was found between the 2 sessions.

fMRI Data

In the hungry-satiated group, during the hungry state, both observation of grasping food and observation of grasping object versus scrambled pictures (GF vs. SP) hungry and (GO vs. SP) hungry were associated with increased activity bilaterally in the EBA, the superior parietal cortex, the superior temporal gyrus, the left inferior parietal lobule, the precentral gyrus, and the inferior frontal gyrus (see Table 1). In addition, specific activation during the observation of grasping food was detected in the amygdala, the orbitofrontal cortex, the parahippocampal gyrus, the hypothalamus, and the fusiform gyrus. All these areas showed diminished relative activity when participants were in a satiated state (i.e., session 2).

In the satiated-satiated group (i.e., [GF vs. SP] satiated and [GO vs. SP] satiated), similar activations to the hungry-satiated group were detected when participants observed grasping food

and grasping objects, except the specific food/motivation-related regions found in the hungry-satiated group (see Table 2).

Motivation Effect on Watching Grasping Food

The regions modulated by the hungry state, for example, (GF-GO) hungry - (GF-GO) satiated, were detected in the inferior frontal gyrus, EBA, and the superior temporal gyrus in addition to the food/motivation-related regions (i.e., amygdala, orbitofrontal cortex, parahippocampal gyrus, hypothalamus, fusiform gyrus) (see Table 3). In particular, neither inferior frontal cortex nor food/motivation-related regions have an evident response after the same analysis at the satiated-satiated group, for example, (GF-GO) satiated - (GF-GO) satiated.

Stimulus Effects Irrespective of Motivation

Conjunction analysis of grasping food versus grasping objects across the hungry and satiated sessions in the hungry-satiated group and across 2 satiated sessions in the satiated-satiated group resulted in specific activation in the inferior occipital cortex and insula irrespective of motivational state. Similarly, activations specific to the grasping objects were found in the parietal and precentral cortex after the conjunction of GO versus GF across 2 testing sessions (see Table 3).

Grasping Food versus Grasping Objects

To test if the BOLD signal increase in these hunger-modulated regions was selective for the observation of grasping food condition, we performed direct comparison between the watching grasping food (GF) and watching grasping objects (GO) conditions, as well as comparison between the hungry-satiated and the satiated-satiated within these ROIs (Fig. 2). In all cases, responses were stronger for observation of grasping food as compared with observation of grasping objects in the hungry state ($P < 0.05$). For the clusters in the left inferior frontal gyrus, such a response became inverted, for example, stronger activation for GO than for GF, at the satiated state (session 2) in the satiated-satiated group. And all clusters had similar responses for the other conditions.

Correlation between VAS and BOLD Response

The BOLD response in the right inferior frontal cortex ($x 48, y 22, z 26$) and left amygdala was significantly correlated with the behavioral measure of the motivation to eat ($P < 0.05$) as provided from the VAS ratings (Figs 3 and 4).

Discussion

Observing grasping food and objects was associated with similar activated regions, including the superior temporal gyrus, the superior and inferior parietal cortex, the post- and precentral gyrus, and the inferior frontal gyrus. This is in accordance with previous neuroimaging studies that have reported the same frontoparietal network activated by grasping observation (e.g., Grafton et al. 1996; Buccino et al. 2001; Grèzes and Decety 2001; Grèzes et al. 2003). These regions constitute the core of the human mirror-neuron system (Rizzolatti and Craighero 2004).

The most interesting finding of the current study was the demonstration that motivation to eat modulated the mirror-neuron system (see Fig. 2). Greater signal change was detected in the inferior frontal gyrus, the superior temporal gyrus, and

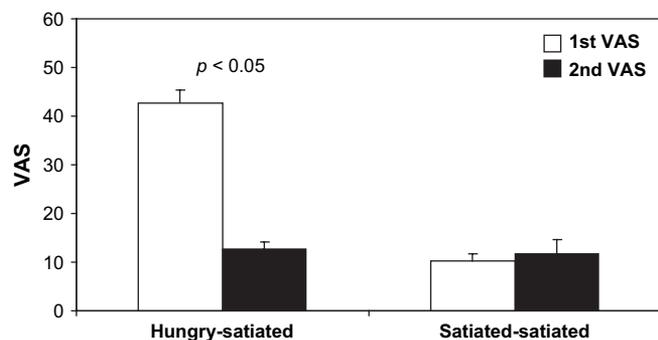


Figure 1. Subjective motivation to eat illustrated by the ratings from the VAS in the 2 groups (hungry-satiated and satiated-satiated) of participants before the first (□) and the second (■) fMRI sessions. The interval (1.5 h) between the 2 sessions was equivalent for every participant from either group.

Table 1Significant hemodynamic signal change during the hungry state of the hungry-satiated group ($P < 0.005$ uncorrected, $k > 10$)

Anatomical location	Hemisphere	MNI coordinates			Z-score	Cluster size
		x	y	z		
Grasping food versus scramble (GF vs. SP)						
Superior temporal gyrus	R	34	6	-22	3.21	12
Amygdala	L	-16	-4	-16	3.75	84
Superior temporal gyrus	L	-32	2	-16	3.1	11
Fusiform gyrus	R	42	-48	-16	3.61	19
Inferior frontal gyrus, pars orbitalis	L	-38	32	-14	3.26	57
Parahippocampal gyrus	R	16	-4	-14	3.23	30
Hypothalamus	R	4	0	-14	3.32	15
Fusiform gyrus	L	-48	-46	-12	3.05	112
Inferior frontal gyrus, pars orbitalis	R	44	26	-10	3.97	82
Lateral occipital cortex (EBA)	R	48	-74	-4	6.69	3355
Lateral occipital cortex (EBA)	L	-52	-72	4	6.33	2554
Inferior frontal gyrus, pars opercularis	R	40	8	34	3.11	18
Inferior parietal lobule	L	-44	-36	44	3.2	20
Precentral gyrus	L	-50	-2	48	2.98	20
Superior parietal cortex	L	-28	-54	70	4.7	467
Superior parietal cortex	R	20	-56	70	3.1	30
Grasping objects versus scramble (GO vs. SP)						
Superior temporal gyrus	L	-36	6	-20	3.14	41
Lateral occipital cortex (EBA)	R	52	-62	4	4.79	791
Lateral occipital cortex (EBA)	L	-50	-64	12	4.94	1046
Inferior frontal gyrus, pars triangularis	L	-52	28	26	3.05	11
Precentral gyrus	R	32	14	38	2.91	12
Inferior parietal lobule	L	-44	-36	44	3.39	95
Superior parietal cortex	L	-32	-54	65	4.04	54
Superior parietal cortex	R	28	-58	67	3.48	20

Table 2Significant hemodynamic signal change during the first satiated state of the satiated-satiated group ($P < 0.005$ uncorrected, $k > 10$)

Anatomical location	Hemisphere	MNI coordinates			Z-score	Cluster size
		x	y	z		
Grasping food versus scramble (GF vs. SP)						
Lateral occipital cortex (EBA)	R	50	-68	-4	5.24	726
Lateral occipital cortex (EBA)	L	-48	-70	8	6.12	1010
Precentral gyrus	L	-50	4	40	3.48	80
Inferior parietal lobule	L	-44	-30	46	3.18	29
Superior frontal gyrus	L	-14	28	62	3.34	24
Superior parietal cortex	R	27	-56	64	4.47	135
Grasping objects versus scramble (GO vs. SP)						
Lateral occipital cortex (EBA)	R	42	-84	-2	5.04	817
Lateral occipital cortex (EBA)	L	-50	-70	10	6.04	851
Superior temporal gyrus	R	50	-62	12	4.31	225
Inferior frontal gyrus, pars triangularis	R	54	26	18	3.08	17
Superior parietal cortex	L	-26	-74	48	4.04	511
Superior parietal cortex	L	-28	-48	76	4.68	154
Superior parietal cortex	R	24	-60	70	3.73	65

the superior parietal cortex when hungry participants were observing the grasping of food as compared with when they were satiated. Further, the hemodynamic response in the right inferior frontal gyrus correlated with subjective assessments of the motivation to eat, as measured by the VAS (see Fig. 3). No such a correlation was detected when participants were observing grasping objects. Animal research has shown that both the inferior frontal and posterior parietal cortices contain mirror-neurons that code the goal of the action. This matching mechanism allows the animal to predict the goal of the observed action. Further, it has been demonstrated that the firing of these neurons can be modulated by the action circumstances (Fogassi et al. 2005). It is worth noting that electrophysiological data from the monkey have not shown an effect of biological salience of the stimuli. Grasping a piece of food or a geometric object produces responses of the same intensity (Rizzolatti and

Craigero 2004). Nevertheless, monkeys are usually rewarded with food during such experiments. Interestingly, our findings are consistent with the study conducted by Ferrari et al. (2005) that showed that the observation of grasping food leads, in monkeys, to social facilitation in the observer. Our data further suggest that the neuro-hemodynamic response in the human homologue regions can also be modulated by the motivational state of the observer.

In fasting participants, presentation of video clips depicting an individual grasping food elicited specific activation in the hypothalamus, amygdala, parahippocampal gyrus, orbitofrontal gyrus, and fusiform gyrus (see Table 3). A number of neuro-imaging studies focusing on the pleasantness or desirability of food cues found activation in the same network, for example, the orbitofrontal cortex, the amygdala, the parahippocampal gyrus, the anterior fusiform gyrus, insula, and the striatum

Table 3Significant hemodynamic changes in the hunger-satiated and satiated-satiated groups ($P < 0.005$, uncorrected)

Anatomical location	Hemisphere	MNI coordinates			Z-score
		x	y	z	
Double-subtraction analysis: hunger-modulated regions					
Hungry-satiated ((GF-GO) hungry - [GF-GO] satiated) masked by (GF-GO) hungry					
Superior temporal gyrus	R	38	16	-26	2.16
Parahippocampal gyrus	L	-18	-14	-22	2.14
Fusiform gyrus	L	-40	-50	-18	3.85
Fusiform gyrus	R	45	-55	-17	3.57
Orbitofrontal gyrus	R	8	38	-16	3.72
Superior temporal gyrus	L	-44	16	-16	2.70
Amygdala	L	-16	-4	-14	2.98
Hypothalamus	R	2	0	-8	3.04
Inferior frontal gyrus	L	-50	26	-2	4.01
Inferior frontal gyrus	R	48	26	-1	3.75
Lateral occipital gyrus (EBA)	R	48	-78	0	4.79
Lateral occipital gyrus (EBA)	L	-48	-76	10	3.98
Superior parietal lobule	L	-28	-76	50	2.74
Satiated-satiated ((GF-GO) satiated - [GF-GO] satiated) masked by (GF-GO) satiated					
Conjunction analysis: grasping food specific regions					
Hungry-satiated (conjoined [GF-GO] hungry and [GF-GO] satiated)					
Inferior occipital gyrus	L	-6	-96	-6	3.35
Inferior occipital gyrus	R	6	-94	8	3.04
Insula	L	-36	0	-8	2.00
Satiated-satiated (conjoined [GF-GO] satiated and [GF-GO] satiated)					
Inferior occipital gyrus	R	6	-76	-12	2.95
Inferior occipital gyrus	L	-6	-96	-10	2.92
Insula	L	-36	0	-8	2.00
Conjunction analysis: grasping objects specific regions					
Hungry-satiated (conjoined [GO-GF] hungry and [GO-GF] satiated)					
Inferior parietal lobule	L	-64	-48	32	2.13
Precentral gyrus	L	-40	-16	48	2.95
Satiated-satiated (conjoined [GO-GF] satiated and [GO-GF] satiated)					
Superior parietal lobule	R	14	-70	52	2.59
Precentral gyrus	L	-32	6	40	2.47

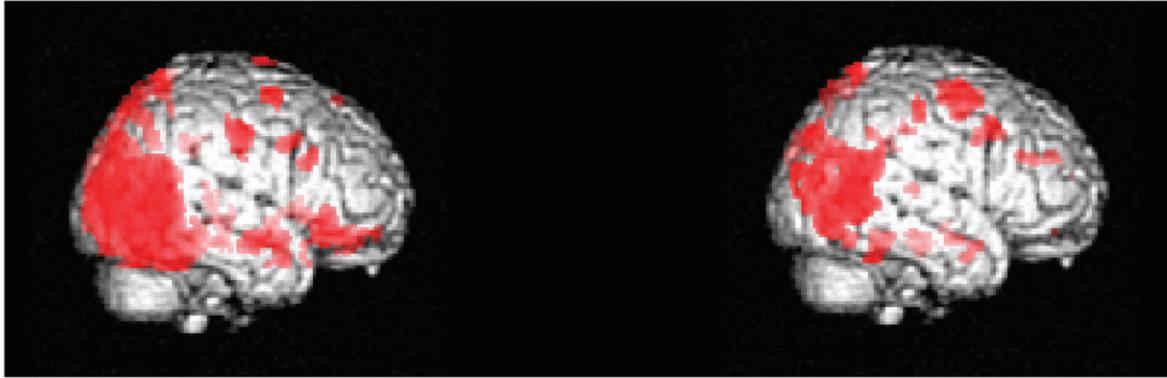
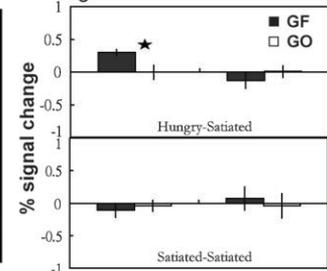
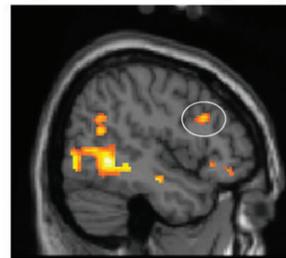
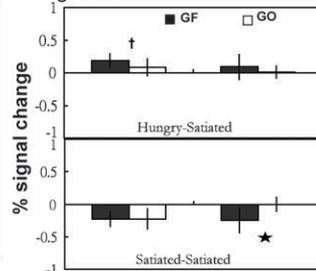
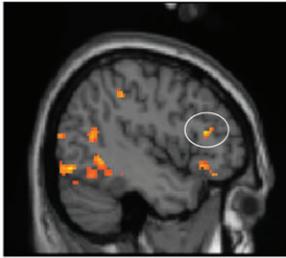
(LaBar et al. 2001; Morris and Dolan 2001; Small et al. 2001; Pelchat et al. 2004; Wang et al. 2004). It was suggested that these regions may function to regulate goal-directed behaviors by signaling sensory cues that are relevant to the motivational needs of the organism (LaBar et al. 2001). The involvement of the hypothalamus and orbitofrontal cortex during hungry state is consistent with animal studies that found food-related responses to be altered by satiation in these 2 regions (e.g., Rolls 1996). In addition, our study found differential activation in the amygdala when hungry participants watched the grasping of food and not when they watched the grasping objects. The hemodynamic response in the amygdala ($x = -16$, $y = 2$, $z = -14$) significantly correlated with the behavioral measure of the motivation to eat, as measured by VAS ($P < 0.05$), when participants watched the grasping of food (Fig. 4). Despite the fact that amygdala has mostly been reported to be associated with negative emotions, there is now some evidence that this region responds to the intensity rather than to the valence of the stimuli (e.g., Anderson et al. 2003; Small et al. 2003). Activation of the amygdala has also been reported when subjects are hungry versus satiated (LaBar et al. 2001) and even when satiated subjects view the names of neutral versus preferred foods (Arana et al. 2003). Overall, this supports the hypothesis that the amygdala plays a role in mediating the real-time significance of food stimuli according to the motivational state of the perceiving organism (Hamann et al. 1999; LaBar et al. 2001).

Interestingly, the EBA was found bilaterally activated both during watching grasping food and watching grasping objects,

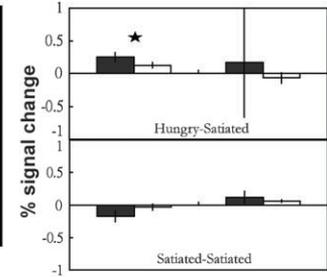
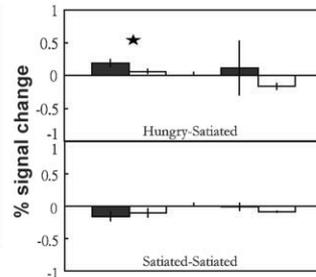
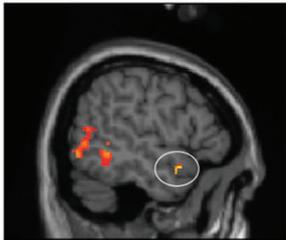
but not during watching slides of food and objects alone (results not shown). This finding is consistent with the role of this area in the visual processing of images of human bodies or body parts (Downing et al. 2001; Grossman and Blake 2002; Chan et al. 2004; Saxe et al. 2005). Moreover, recent fMRI studies indicate that EBA responds not only to the perception of other people's body parts but also during goal-directed movements produced by the observer, even in the absence of visual feedback from her/his movements (Astafiev et al. 2004; Jackson et al. 2006). These authors thus proposed an extended role for the EBA, involving not only the visual perception of body parts but also in the planning, execution, and imagination of actions with different limbs.

Conclusion

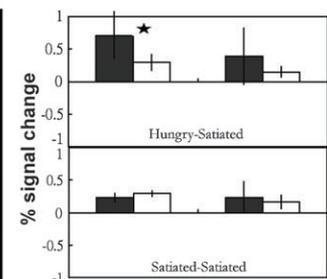
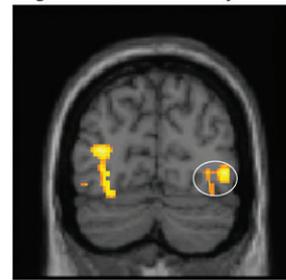
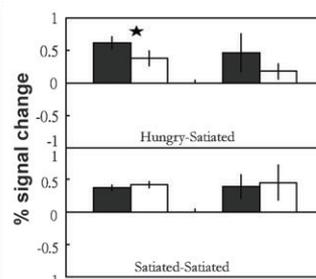
This is the first study that investigated and demonstrated that motivation can influence activity in the human mirror-neuron system. As predicted, the desire to eat leads to hemodynamic modulation not only in the neural circuitry involved in drive and motivation but also in the regions that are part of the mirror-neuron system, particularly the inferior frontal gyrus. This indicates that the motivational state of the organism affects neural systems involved in perception-action coupling mechanism. We speculate that the signals arising from the neural systems involved with drive (orbitofrontal cortex) and motivation (amygdala) enhance the activity in the mirror-neuron system to prepare the organism to behave (in this study, feeding behavior) in order to restore its homeostasis. Finally, our

A**OBSERVATION
grasping food****OBSERVATION
grasping objects****B** Left inferior frontal gyrus, *pars triangularis*Right inferior frontal gyrus, *pars triangularis***C** Left superior temporal gyrus

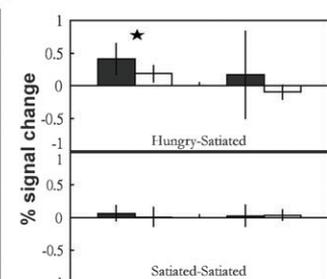
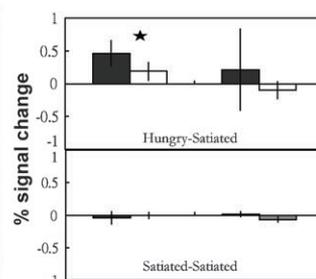
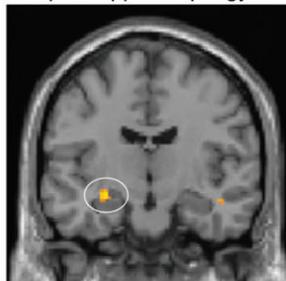
Right superior temporal gyrus

**D** Left extrastriate body area

Right extrastriate body area

**E** Left parahippocampal gyrus

Right parahippocampal gyrus



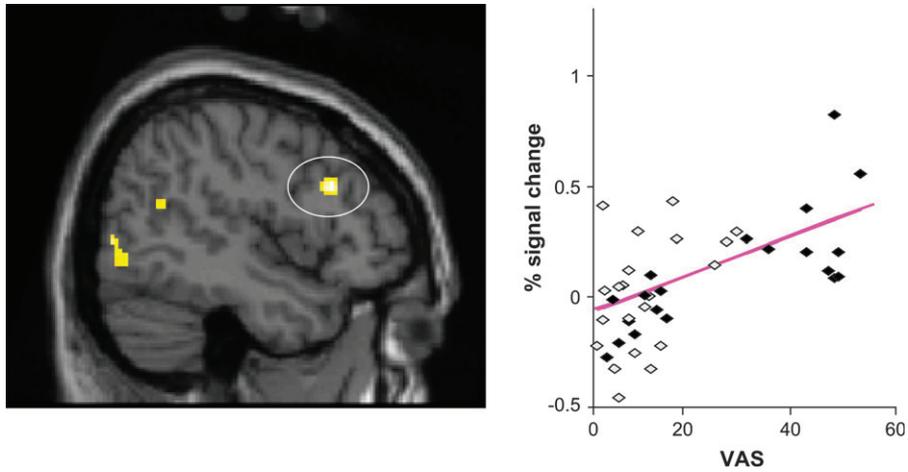


Figure 3. Significant correlation ($r = 0.38, P < 0.01, n = 40$) between the percentages of signal change in the right inferior frontal gyrus (x 48, y 22, z 26) during the observation of grasping food and the self-report ratings of hunger (VAS); \blacklozenge , hungry-satiated group; \diamond , satiated-satiated group.

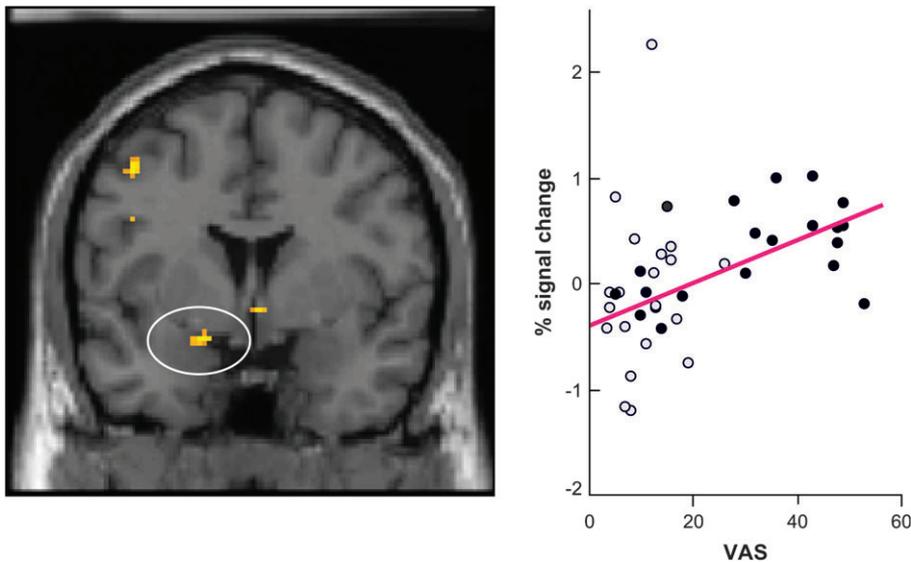


Figure 4. Significant correlation ($r = 0.36, P < 0.05, n = 40$) between the percentages of signal change in the left amygdala (x -16, y 2, z -14) during the observation of grasping food and self-report rating of hunger (VAS); \bullet , hungry-satiated group; \circ , satiated-satiated group.

findings open up new direction in the investigation of the adaptive functions of the mirror-neuron system by showing that affordances from the external environment are determined not only by their physical properties but also by their internal state of the organism.

Notes

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Figure 2. (A) Commonalities and differences between the observation of grasping food and the observation of grasping objects across the hungry and satiated condition. (B) Group average activation of left and right inferior frontal gyrus superimposed on sagittal sections of the MNI brain. Histograms show the percent signal change at the local maxima in left (-44, 28, -16) and right inferior frontal gyrus (48, 20, 28) across the hungry and satiated conditions; the white histogram corresponds to observing grasping food (GF), the black to observing grasping objects (GO); $^{\dagger}P \sim 0.05$; $*P < 0.05$. (C) Group average activation of left (-52, 10, -16) and right superior temporal gyrus (55, 12, -14) superimposed on sagittal sections. Histograms show the percent signal change at the local maxima in left and right superior temporal gyrus across the hungry and satiated conditions; other conventions as in (B); $*P < 0.05$. (D) Group average activation of left (-56, -60, 10) and right EBA (46, -76, -2) superimposed on coronal sections. Histograms show the percent signal change at the local maxima in left and right EBA across the hungry and satiated conditions; other conventions as in (B); $*P < 0.05$. (E) Group average activation of left (-28, -12, -12) and right parahippocampal gyrus (22, -22, -14) superimposed on coronal sections. Histograms show the percent signal change at the local maxima in left and right parahippocampal gyrus across the hungry and satiated conditions; other conventions as in (B); $*P < 0.05$.

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