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Harold Mouras, S. Stoléru, V. Moulier, M. Péligrini-Issac, R. Rouxel, et al.. Activation of mirror-neuron system by erotic video clips predicts degree of induced erection: an fMRI study. *NeuroImage*, 2008, 42 (3), pp.1142-1150. 10.1016/j.neuroimage.2008.05.051 . hal-03649712

HAL Id: hal-03649712

<https://u-picardie.hal.science/hal-03649712>

Submitted on 8 Sep 2023

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Activation of mirror-neuron system by erotic video clips predicts degree of induced erection: an fMRI study

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Although visually-induced erection is a common occurrence in human male behaviour, the cerebral underpinnings of this response are not well-known. We hypothesized that the magnitude of induced erection would be linearly correlated with the activation of the mirror-neuron system in response to sexually explicit films. When presented with sexual video clips, eight out of ten healthy subjects had an erectile response demonstrated through volumetric penile plethysmography. The level of activation of the left frontal operculum and of the inferior parietal lobules, areas which contain mirror neurons, predicted the magnitude of the erectile response. These results suggest that the response of the mirror-neuron system may not only code for the motor correlates of observed actions, but also for autonomic correlates of these actions.

Introduction

Although visually-induced erection is a common occurrence in human male behaviour, the cerebral underpinnings of this response are not well-known. Similarly, in spite of the very large usage of visual erotica – the American pornography industry generates an estimated \$10 billion in annual sales (<http://members.aol.com/smartnews/hm04.htm>, visited on June 17, 2006) – the neural mechanisms of erotica-induced erections are largely unknown. Among visual erotica, movies depicting sexual interactions occupy a prominent place. The very first studies on the brain responses to visual sexual stimuli (VSS) (Stoléro et al., 1999; Bocher et al., 2001) suggested that the observation of video clips depicting sexual interaction induces an activation of the mirror-neuron system. Similarly, it has been suggested that the presentation of static (photographic) VSS triggers action representations of sexual

behavior mediated by the mirror-neuron system (Ponseti et al., 2006). Furthermore, in response to photographic VSS, the BOLD signal in the pars opercularis of the inferior frontal gyrus, a prominent part of the mirror-neuron system, was found to be correlated with the penile volumetric response (Moulrier et al., 2006).

Mirror neurons are a particular class of visuomotor neurons, originally discovered in area F5 of the monkey premotor cortex, that discharge both when the monkey performs a particular action and when the monkey observes the same action performed by another animal (monkey or human) (Rizzolatti and Craighero, 2004). The notion of a mirror-neuron 'system' has arisen because neurons from several different areas, including the posterior part of the inferior frontal gyrus, the lower part of the precentral gyrus, and the rostral part of the inferior parietal lobule, display the properties of mirror neurons (Rizzolatti and Craighero, 2004). That a brain area belongs to the mirror-neuron system does not mean that all its neurons display the properties of mirror neurons; only a fraction of neurons [e.g., 25% of studied neurons in area F5 (Rizzolatti and Craighero, 2004)] display such properties.

Two main hypotheses have been advanced on what might be the functional role of mirror neurons: (i) mirror-neuron

Abbreviations: VSS, Visual Sexual Stimuli; VPP, volumetric penile plethysmography; BA, Brodmann area.

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activity mediates imitation (Jeannerod, 1994); (ii) mirror neurons are at the basis of action understanding (Rizzolatti et al., 2001). Several functional neuroimaging studies and one study based on repetitive transcranial magnetic stimulation support the hypothesis that mirror neurons are activated by tasks where subjects are required to imitate an action that is already present in their repertoire (reviewed in Iacoboni, 2005). While it has been proposed that mirror neurons mediate imitation of actions, in most cases subjects do not perform actions they observe in other individuals. When observers see a motor event that shares features with a similar motor event present in their motor repertoire, they are thought to be only primed to repeat it. The greater the similarity between the observed event and the motor event, the stronger the priming is (Rizzolatti and Craighero, 2004). In addition, two studies indicate that mirror neurons participate in imitative learning, i.e., the acquisition of a new motor skill based on the observation of an action presented as a model (Buccino et al., 2004; Vogt et al., 2007). However, there is vast agreement among ethologists that imitation, the capacity to learn to do an action from seeing it done, is present only in humans and probably in apes (Visalberghi and Frigaszy, 2001). Because mirror neurons have been found in other species, the primary function of mirror neurons cannot be action imitation.

The validity of the proposed function of mirror neurons in action understanding was tested in an experiment where discharges of mirror neurons were recorded as monkeys were presented with a meaningful action (grasping action directed to a piece of food) and with a meaningless one (grasping action directed to nothing) (Umiltà et al., 2001). The experimental paradigm made possible for the visual features of meaningful and meaningless actions to be identical. Mirror neurons responded when the monkey was presented with meaningful actions but not when it was presented with meaningless actions. To explain how mirror neurons mediate understanding of actions done by others, the proposed mechanism is the following (Rizzolatti et al., 2001). Each time an individual sees an action done by another individual, neurons that represent that action are activated in the observer's premotor cortex. This automatically induced motor representation of the observed action corresponds to that which is spontaneously generated during active action and whose outcome is known to the acting individual. Thus, the mirror neuron system transforms visual information into knowledge. In other words, this proposed function of mirror neurons in a given monkey (monkey A) is to assign a meaning to a motor act seen performed by another animal, monkey B; in addition, this meaning is assigned through a reference of monkey A to itself: monkey B is doing what monkey A is doing when these particular neurons are firing.

The responses of mirror neurons have not been observed to vary with motivational significance - for example, viewing an experimenter grasping a piece of food or a geometric solid produces responses of the same intensity. In addition, it is of little importance for neuronal activation if the observed action is eventually rewarded: the discharge of mirror neurons is of the same intensity if the experimenter grasps the food and gives it to the recorded monkey or to another monkey. However, a recent study has indicated that hunger modulates the response of mirror neurons to the observation of another person grasping food (Cheng et al., 2006), suggesting that there may be interplay between neural systems for motivation and action observation.

This possibility is also suggested by work expanding the concept of mirror neurons to account for the experience of the affective states of other persons (Carr et al., 2003; Gallese, 2003) or the understanding of others' intentions (Iacoboni et al., 2005). Thus, motivational level could modulate the response of the mirror-neuron system and reciprocally the stimulation of this system could influence motivational processes. In the area of sexual motivation, observation of VSS might induce the activation of the neural network that responds to the observation of any kind of human action, but with the added particularity that observation of sexual actions could induce the corresponding motivational state.

Our specific hypothesis was that the mirror-neuron system participates in the mediation of sexual arousal, including erectile responses, induced by the observation of sexual actions represented in VSS. Experimental studies indicate that action observation or motor imagery, i.e., a mental rehearsal of motor acts that is not accompanied by overt body movements, induce autonomic responses. In subjects observing weight lifting movements, autonomic nervous system responses (skin resistance, temperature, and heart rate) were significantly higher and longer when the weight lifted was 90% of each participant's personal best mark than when it was 50% of that best mark (Bolliet et al., 2005). Decety et al. (1991) measured cardiac and respiratory activity during mental simulation of locomotion at increasing speed and revealed a covariation of heart rate and pulmonary ventilation with the degree of imagined effort. Similar results have been reported by other groups (Oishi and Maeshima, 2004; Fusi et al., 2005). Likewise, mental imagery of sexual activity is an important determinant of sexual arousal, including erection (Smith and Over, 1991). As detailed hereunder, a neural pathway linking the mirror-neuron system to neural structures controlling erection could be represented by the efference of the frontal operculum - a region containing mirror neurons - to the insula (Augustine, 1996; Mufson and Mesulam, 1982).

To investigate the hypothesis that the activation of the mirror-neuron system could be part of the neural mechanisms regulating visually-induced sexual arousal, including the erectile response, we examined whether the response of the mirror-neuron system to sexually stimulating video clips is correlated with the erectile response of healthy volunteers. In addition, based on findings of the brain responses to photographic VSS (Moulier et al., 2006), we hypothesized that the level of erection would predict the magnitude of the BOLD response in primary and secondary somatosensory areas corresponding to the penis. If, indeed, these somatosensory areas correspond to the penis, then increasing afferent signals related to increasing erection should result in a rising BOLD signal in these areas. Accordingly, specific hypotheses were made regarding the relative time courses of the penile and cerebral responses: the responses of the mirror-neuron system were hypothesized to start before, and then to lead, the genital response; conversely, erection was hypothesized to start before, and then to lead, corresponding cerebral somatosensory responses.

Materials and methods

Participants

Subjects were recruited through posters affixed on university premises. The eligibility criteria were male gender,

ages 18 to 60, right handedness, heterosexual orientation, no visual problems, no current or previous psychiatric, sexual and/or physical disease or medical treatment, no metallic material in the body, and no claustrophobia. To make sure that potential participants fulfilled the criteria, they were examined physically and were presented with the Composite International Diagnostic Interview (CIDI; Organisation Mondiale de la Santé, 1996) sections on anxiety disorders, alcohol-related disorders, and other substance-related disorders (categories of disorders selected because of their prevalence in the targeted population of students), the Symptom Checklist-90 Revised (SCL-90R; Derogatis, 1977), and the 13-item version of the Beck Depression Inventory (Beck and Beck, 1972). Heterosexual orientation was assessed through the ACSF questionnaire (Spira et al., 1993) and the Brief Sexual Function Questionnaire (Reynolds et al., 1988). The latter questionnaire was also used to screen out sexual dysfunctions. The Sexual Interest Score (Bancroft et al., 1974) and the Sexual Arousal Inventory (Hoon et al., 1976) adapted to males were used to assess sexual motivation and arousability. Handedness was assessed through the Edinburgh Inventory (Oldfield, 1971). In addition, the penile circumference of each potentially eligible subject was measured, in order to subsequently adapt the penile plethysmograph (see below). The local ethics committee (Pitié-Salpêtrière) approved the study and subjects gave their written informed consent after complete description of the study. Subjects' intimacy was ensured by following published guidelines (Rosen and Beck, 1988).

Experimental design and stimuli

The study was based on a blocked design comprising three experimental conditions defined by three types of silent video clips: emotionally neutral documentary clips (N condition), sexually explicit films depicting heterosexual intercourse (S), and humorous clips, inducing a pleasant but nonsexual emotion (H condition). Essentially, the first S clip depicted a man caressing a female partner with his right hand, the second clip showed fellatio, and the third showed intercourse. We presented humorous clips to demonstrate that potential differences in brain activation between the S and the N conditions were related to sexual arousal and not to emotional arousal per se. In an attempt to control for the perception of moving and interacting persons appearing in S films, N and H films also displayed moving and interacting persons. For each of the three experimental conditions, three different clips were presented, so that an experimental run comprised nine successive blocks. More precisely, the run comprised: (i) firstly, a 20-s white screen block; (ii) nine experimental blocks lasting 50 s each; (iii) a final 20-s white screen block. Each stimulation block was separated from the following by a 10-s white screen presentation to allow experimenters to discriminate effects of the termination of blocks from those of the beginning of blocks. Across subjects, the different experimental conditions were presented in a pseudo-random order. However, in order to avoid habituation effects the same experimental condition was never assigned to two consecutive blocks. To check that subjects did pay attention to the stimuli, we inserted within one randomly selected clip of each condition a 100 ms-long orange screen. The subjects were instructed to press a keyboard button upon seeing this screen.

Measures

MRI acquisitions

Acquisitions were performed on a 1.5 Tesla Signa scanner (GE Medical Systems, Milwaukee, WI) in the following order: (i) a sagittal structural acquisition that allowed positioning axial slices over the brain; (ii) a 3D high-resolution structural acquisition (3D-SPGR T₁-weighted sequence; 124 contiguous axial 1.5 mm-thick slices; TE=14 ms; TR=300 ms; field of view=24 cm; 256×192 matrix); and (iii) a functional run using a T₂^{*}-weighted echoplanar (EPI) gradient echo sequence (20 contiguous 6 mm-thick axial slices; TE=60 ms; TR=5 s; flip angle=90°; field of view=24 cm; 64×64 matrix; in-plane resolution=3.75×3.75 mm).

Volumetric penile plethysmography (VPP)

Whereas at high levels of erection, both penile circumferential and penile volume phallometry measures are highly correlated, at low levels of response volumetric phallometry is a more accurate measure of erection (Kuban et al., 1999). Therefore, in the present study we used a volumetric method to better capture the cerebral correlates of initially low levels of penile tumescence. The apparatus was derived from a volumetric penile plethysmograph described previously (Freund et al., 1965). Briefly, after the subject had introduced his penis into a plastic cylinder, pressure variations of the air inside the cylinder caused by penile volume increases were converted into a digitized signal recorded on a PC.

Rating scales

After the functional run, single-item scales, ranging from 1 (totally absent or extremely low) to 9 (extremely high), were presented to assess seven categories of subjective feelings and perceptions experienced during the run: beauty of the women presented on the films, perceived desire to engage in sexual behavior, perceived degree of erection, feeling of pleasure, feeling of displeasure, interest for photographs, feeling of humor.

Experimental procedure

Video clips, as well as the subsequently presented scales, were projected on a translucent screen through a video projector located in the scanner control room. Subjects could see the screen through a mirror fixed on the head-coil. To limit movements, foam padding was placed on both sides of the head. A keyboard was fixed on the subject's abdomen and linked through an optic fiber to an LED located in the scanner control room. Finally, subjects were debriefed using a semi-structured interview.

Data analysis

A repeated measures analysis of variance of subjective ratings was performed using SPSS® 14 software (Chicago, IL). Functional data preprocessing steps (Friston et al., 1995a) and statistical analyses (Friston et al., 1995b; Friston et al., 1995c) were performed using the SPM99 software package (Wellcome Department of Cognitive Neurology, London, UK; see <http://www.fil.ion.ucl.ac.uk/spm99.html>).

Data preprocessing

The first two functional brain volumes were discarded to allow for T₁ equilibrium effects. For each subject, head-motion was

Table 1
Plethysmographic and psychological responses to the three experimental conditions

Responses	Condition		
	Neutral	Humorous	Sexual
Penile plethysmography**	-0.1 (0.1)	0.0 (0.1)	0.2** (0.1)
Perceived erection***	1.2 (0.1)	1.2 (0.1)	5.1*** (0.7)
Beauty***	1.4 (0.3)	1.7 (0.3)	6.6*** (0.3)
Desire***	1.1 (0.1)	1.3 (0.2)	6.5*** (0.5)
Pleasure***	2.2 (0.5)	4.1* (0.8)	6.6*** (0.4)
Displeasure**	4.1 (0.8)	1.7* (0.4)	1.3* (0.2)
Interest***	2.7 (0.4)	4.8*** (0.6)	6.1*** (0.5)
Perceived humor***	1.9 (0.3)	5.0** (0.8)	1.3 (0.2)

Notes. The penile plethysmographic measure is the mean value (SD) of the time derivative of the plethysmographic signal of the eight subjects presenting an erection during the run. Time derivative: amount of change of the plethysmographic measure over each TR. For scaling of plethysmographic measure, see Methods. Rated perceptions [means (SDs), $n=10$]: (1) perceived degree of erection, (2) beauty of the characters appearing in the clips, (3) perceived desire to engage in sexual behavior, (4) feeling of pleasure, (5) feeling of displeasure, (6) interest for clips, (7) feeling of humor. P levels after names of variables (e.g., Beauty) refer to repeated-measures ANOVA; P levels after means refer to pairwise comparison of conditions with the neutral condition as the reference condition.

* $p < .05$.

** $p < .01$.

*** $p < .001$.

assessed using a six-parameter rigid-body affine transformation. To optimize the correspondence between structural and functional data, coregistration parameters were estimated by maximizing the mutual information between the 3D structural run and the mean functional image (Maes et al., 1997). Then, these coregistration parameters were applied to all functional images.

Functional and structural brain images were spatially normalized into the stereotactic space of the Montreal Neurological Institute (MNI) using a 12-parameter affine/nonlinear transformation. Finally, all functional images were spatially smoothed with an eight-millimeter full-width-at-half-maximum (FWHM) isotropic Gaussian kernel for the group analysis.

Statistical analysis

To identify brain regions where the BOLD signal was correlated with the VPP response, a fixed-effects correlational group analysis was conducted on the eight subjects who presented an erectile response. Each individual VPP response was processed as follows: (i) pressure values corresponding to the discarded functional volumes were also discarded; (ii) as the sampling frequency of the plethysmograph was higher (20 Hz) than that of the MRI scanner (0.2 Hz), each set of 100 consecutive plethysmographic values was replaced by its mean value, yielding a time series referred to hereunder as the plethysmographic regressor, with one pressure value for each functional volume; (iii) this time series was then scaled by subtracting from the series the mean value of the plethysmographic signal and dividing the resulting series by the maximum value of the signal.

Two kinds of hypotheses were made about the correlation between the regional BOLD signal and the plethysmographic measure. Firstly, for the mirror-neuron system, variations of the BOLD signal were hypothesized to precede those of the plethysmographic signal. The time lag between the two

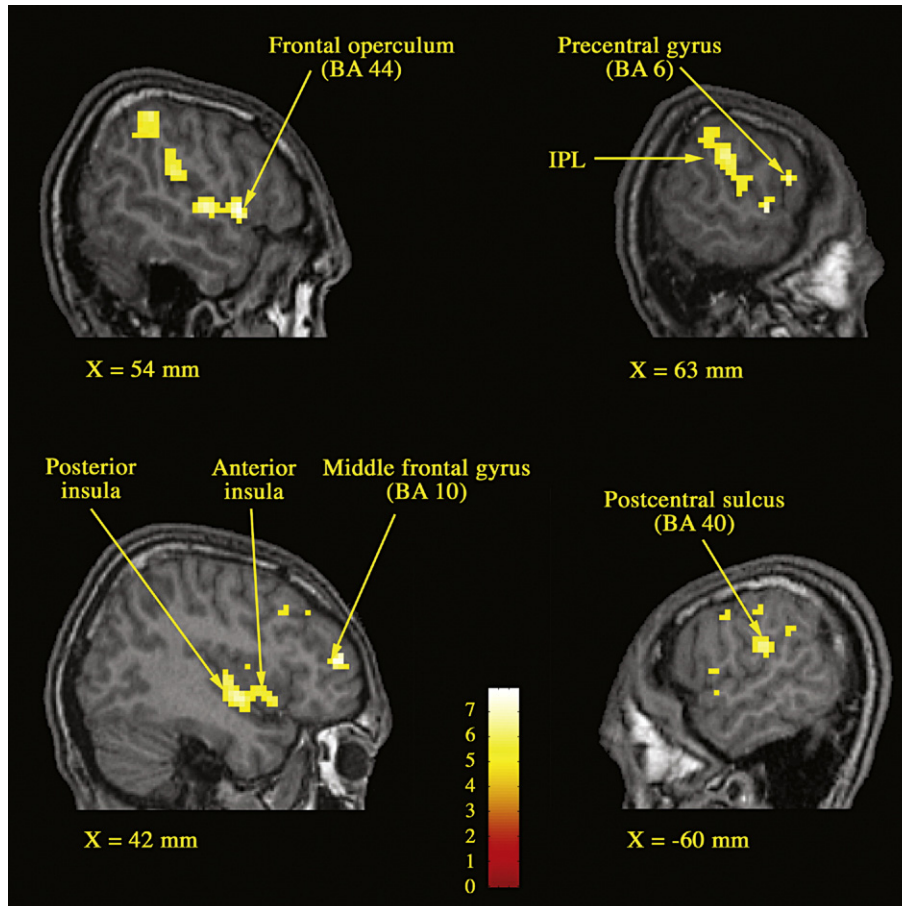


Fig. 1. Parasagittal sections showing brain areas where the fMRI signal was correlated with the concurrent penile volumetric response. Notes. x refers to the distance in millimeters from the sagittal plane. Height threshold: $p < .05$, corrected for multiple comparisons. Abbreviation: BA: Brodmann area; IPL: inferior parietal lobule.

signals was hypothesized to be equal to the delay between the beginning of stimulus presentation and the start of the erectile response. Therefore, to test this hypothesis, the plethysmographic regressor was correlated with the antecedent BOLD signal, with a lag equal to the interval between the start of the VSS and the beginning of erection. Thus, we tested the correlation between the values of the BOLD signal and the values of the VPP signal recorded after the above mentioned interval. Conversely, for the primary and secondary somatosensory cortices corresponding to the penis, variations of the BOLD signal were hypothesized to follow those of the plethysmographic signal. To test this hypothesis, for each subject the BOLD signal was correlated with the plethysmographic regressor measured 5s, 10s and 20s earlier. The threshold for statistical significance was set to $p < 0.05$, corrected for multiple comparisons.

Results

Plethysmographic responses

Plethysmographic responses were recorded for sexual (S), neutral (N) and humor (H) conditions. Compared with the N condition, the time derivative of the plethysmographic signal was higher in response to the S condition ($F[1, 7]=15.68$; $p < .01$) (Table 1). The time derivative was computed as the amount of change (slope) of the plethysmographic signal over 5s, i.e., the length of the repetition time (TR). We analyzed the time derivative instead of the raw signal because the raw measure often remained elevated after the end of the sexual condition block, obscuring between-conditions differences. The mean delay between the beginning of the sexual clips and the start of the VPP signal increase was 20 s. Therefore, 20 s was the time lag used in correlational analyses performed to identify brain responses occurring before a measurable penile response (see Material and methods).

Self-report measures

Ratings for the sexual (S), neutral (N) and humor (H) conditions are reported in Table 1. Compared with the N condition, higher ratings were recorded in response to the S condition for perceived degree of erection ($F[1, 9]=37.1$; $p < .001$), perceived beauty ($F[1, 9]=156.0$; $p < .001$), perceived desire to engage in sexual behavior ($F[1, 9]=99.4$; $p < .001$), feeling of pleasure ($F[1, 9]=53.8$; $p < .001$), and feeling of interest ($F[1, 9]=30.0$; $p < .001$) as well as lower ratings for feeling of displeasure ($F[1, 9]=10.8$; $p < .05$). For the S condition, the mean (\pm SD) rating of perceived degree of erection was 5.1 (± 0.7), with "5" meaning "Moderate degree of perceived erection". Compared with the N condition, higher ratings were recorded in response to the H condition for feeling of humor ($F[1, 9]=26.3$; $p < .01$).

On debriefing, all eight subjects reported that sexual clips induced a desire to perform a sexual activity or the desire "to take the place of the man appearing in the clips" or the desire to "reproduce" what they were seeing. Six (75.0%) reported experiencing sexual motor imagery, i.e. imagined they were performing actions of a sexual kind, while watching the scenes of sexual interaction.

Brain areas correlated with penile response

The brain areas relevant to the mirror-neuron system and to penile somatosensory areas identified through the correlational analyses are presented in Fig. 1 and Table 2 (see exhaustive list of regions in Tables 1 and 2 of the online electronic supplementary material). In addition, so-called glass brains present an overview of areas where the BOLD signal was correlated with the concurrent VPP signal (Fig. 2) and with the VPP signal recorded 20 s later (20s-lagged) (Fig. 3). In the analysis with no lag between the two signals, strong correlations were recorded in the right frontal operculum (BA

Table 2
Mirror-neuron system and somatosensory areas where the BOLD signal was correlated positively with the plethysmographic signal

Brain area	BA	Non lagged plethysmographic signal		Lagged plethysmographic signal	
		Left hemisphere	Right hemisphere	Left Hemisphere	Right Hemisphere
Frontal operculum	44	~	/	~	/
	44	~	/	~	/
	44	~	~	-51 12 15 (5.48)	/
	9/44				39 9 30 (4.75)
Precentral gyrus	6	~	/	-48 3 3 (6.08)	/
Middle frontal gyrus	6	~	/	-30 0 51 (5.60)	/
	10	~	/	~	/
Postcentral gyrus	1	~	/	~	/
	2	~	/	-60 -21 27 (7.84)	/
	3	~	/	~	/
	40	-51 -27 21 (5.26)	/	~	/
	43	-54 -18 21 (5.82)	/	~	/
Inferior parietal lobule	40	-60 -27 21 (6.37)	/	~	/
	40	~	/	~	/
Postcentral sulcus		~	/	-51 -33 48 (6.05)	/
Supramarginal gyrus	40	-54 -45 33 (5.77)	/	~	/
Anterior insula		-42 3 6 (7.75) -33 18 0 (6.41)	/	-39 12 -9 (5.19)	/
Posterior insula		~	/	-42 -6 -6 (4.95)	/

Notes. The lagged signal refers to the plethysmographic signal recorded 20 s after the fMRI signal. The non-lagged signal refers to the concurrent signal (lag=0s). For each region, the three coordinates (expressed in millimeters) are defined in the MNI stereotactic space (Montreal Neurological Institute, Canada) and refer to the anterior commissure. x positive=right; y positive=anterior; z positive=above. The number in brackets corresponds to the Z statistic of the maximum of the region. Statistical threshold: $p < .05$, corrected. The regions presented in this table are those considered in the Results and Discussion sections of the paper. See online electronic supplementary material (Tables 1 and 2) for an exhaustive list of the regions.

Abbreviations: BA=Brodman area. For each region, slashes (/) separate the left- and right-hemisphere coordinates, with the tilde (~) meaning absence of correlation in one hemisphere.

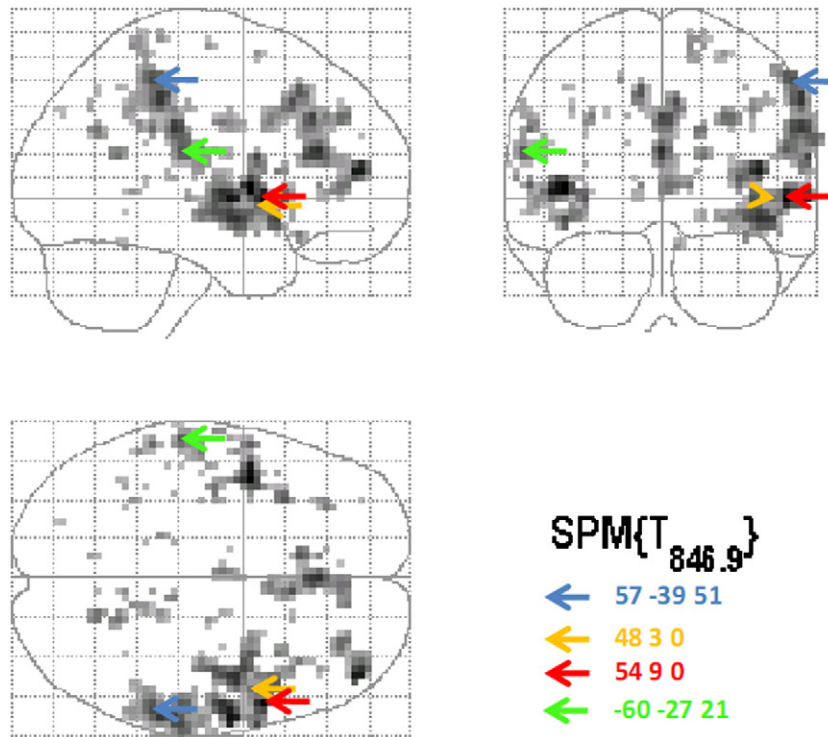


Fig. 2. The glass brain shows a t-map ($p < .05$, corrected), giving an overview of the brain regions where the BOLD signal was correlated with the concurrent volumetric plethysmographic signal (lag=0s). Arrows point to maxima located in the frontal operculum and in the parietal lobule, two regions that contain neurons belonging to the mirror-neuron system.

44), right precentral gyrus (BA 6), right middle frontal gyrus (BA 10), postcentral gyri (BA3, BA40, BA43), inferior parietal lobules (BA 40), left supramarginal gyrus (BA 40), and bilateral insulae. In the analysis with a 20-s lag between the two signals

(the BOLD signal correlated with VPP recorded 20 s later), correlations were again found in the above-mentioned areas, except in BA 43 and the supramarginal gyrus. To show the differential strength of the correlation obtained at various

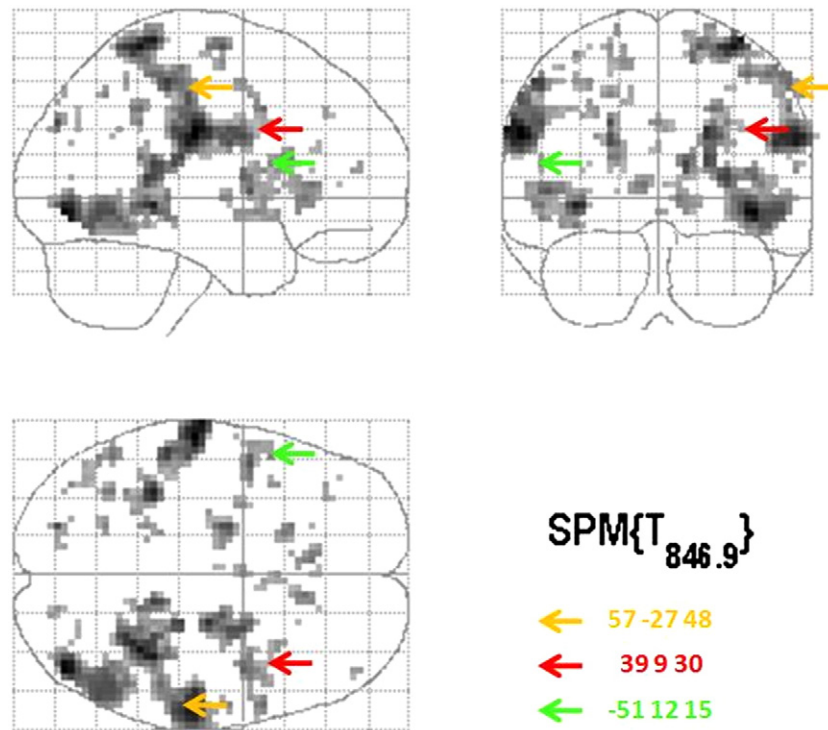


Fig. 3. The glass brain shows a t-map ($p < .05$, corrected), giving an overview of the brain regions where the BOLD signal was correlated with the volumetric plethysmographic signal as recorded 20 s later (lag=20s). Arrows point to maxima located in the frontal operculum and in the parietal lobule, two regions that contain neurons belonging to the mirror-neuron system.

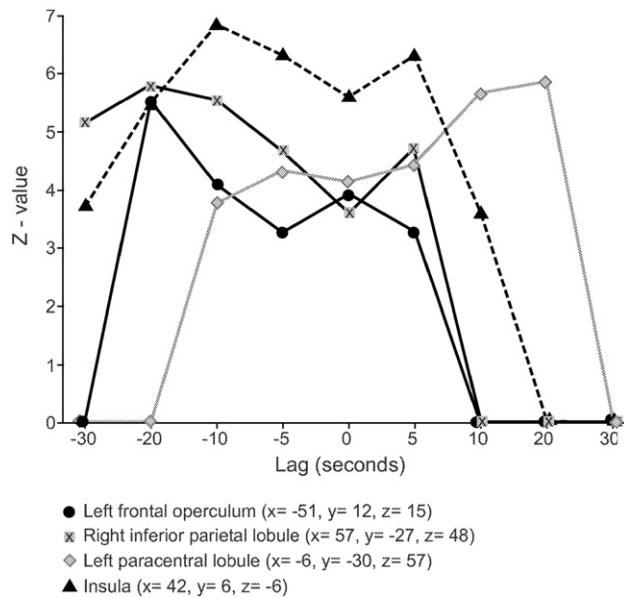


Fig. 4. Correlation profiles between BOLD and plethysmographic signals as a function of the lag between the two signals. Notes: the vertical axis represents the Z statistic associated with the correlation coefficient between the two signals, and the horizontal axis the lag, which is the time interval (seconds) by which the correlated values are separated. Positive lags are those where the plethysmographic response was correlated with subsequent values of the BOLD signal.

lags, for six areas we present the Z values of the positive correlation obtained for nine different lags (Fig. 4). For the left frontal operculum and the right inferior parietal lobule, two regions that contain neurons belonging to the mirror-neuron system, the strongest correlations were found with the BOLD signal preceding the VPP signal by 20s.

The BOLD signal in some regions of the primary somatosensory cortex was correlated with the plethysmographic response. In the paracentral lobules, the plethysmographic response predicted the BOLD signal recorded later, i.e., at lags 5s ($x, y, z = -6, -30, 57, Z = 4.51$), 10s ($x, y, z = -6, -30, 57, Z = 5.75$), and 20s ($x, y, z = -6, -27, 57, Z = 6.81$; and 6, -27, 54, $Z = 4.33$) (Fig. 4). Conversely, correlations of the VPP response were far lower with the BOLD response recorded concurrently with, or before, the VPP, at lags 0, -10s, -20s (as a convention, for negative lags, BOLD signal precedes VPP) (Fig. 4). In addition, a profile with two peaks around zero lag was observed for the Z statistic in the secondary somatosensory cortex ($x, y, z = -54, -18, 21$, and 60, -12, 21) and the right insula ($x, y, z = 42, 6, -6$; Fig. 4). Finally, bilaterally in the lower part of BA2 ($x, y, z = -60, -21, 27$, and 60, -24, 24), regions corresponding to the primary somatosensory cortex of the mouth and hands, the maximum correlation was found with the VPP preceding the BOLD signal by 30s (left BA2, $Z = 8.87$) and by 5s (right BA2, $Z = 7.33$).

Activated brain regions showed by subtractive analyses contrasting the experimental conditions are presented in Table 3 of electronic supplementary materials.

Discussion

In response to video excerpts of sexual interaction, the level of activation of the areas comprising the mirror-neuron system was correlated with the amplitude of penile erection. This result is consistent with the activation of these areas in response to sexual video clips (Stoléru et al., 1999) and with

the correlation between the level of activation of these areas and the level of penile erection in response to photographic sexual stimuli (Moulier et al., 2006).

In the case of hunger, an increased level of motivation was found associated with a higher response of the regions of the mirror-neuron system to video clips depicting a human being grasping food (Cheng et al., 2006). Here, in the area of sexuality, by demonstrating a correlation between the activation of the regions of the mirror-neuron system and the level of penile response, we have shown that, in a reciprocal manner, increasing levels of activation of the mirror-neuron system regions in response to viewing motivationally relevant actions predict increasing levels of sexual arousal in the observer, an index of sexual motivation. Thus, this set of studies suggests the concept of a positive feedback loop, as motivational state may increase the response of mirror neurons, while the response of these neurons could further increase the level of motivation. Hereunder, for each area correlated with the VPP signal, we discuss its implication in the mirror-neuron system and its relation with sexual motivation and behavior.

In the pars opercularis of the inferior frontal gyri, the BOLD signal was positively correlated with the VPP signal measured 20 s later. Pars opercularis (Brodmann area [BA] 44) is a likely homologue of a subdivision of area F5 of monkeys (Binkofski et al., 2000; Binkofski and Buccino, 2004; Hanakawa et al., 2003; Rizzolatti and Arbib, 1998). As detailed in the Introduction, area F5, i.e., the rostral part of the ventral premotor cortex, contains neurons that discharge both when the monkey grasps or manipulates objects and when it observes the experimenter making similar actions.

The response of the frontal operculum, an area that contains mirror neurons, is consistent with six subjects reporting sexual motor imagery in response to the clips. Imagery focused on those motor acts the subjects said they wanted to perform and/or they had previously performed. The response of the frontal operculum is consistent with studies showing that this area is involved in mediating motor imagery of actions (Binkofski et al., 2000; Buccino et al., 2006).

However, in the present experiment the behavioral response consisted not only in sexual motor imagery and the desire to perform sexual actions, but also in an erectile response. Interestingly, for some areas containing mirror neurons, e.g., the left frontal operculum (BA 44), the highest correlation between the BOLD and the VPP signals was obtained when the BOLD signal preceded the VPP signal by a 20-s lag. Is there any evidence that the correlation between the BOLD response in left BA 44 and the subsequent plethysmographic response may be mediated by direct or indirect pathways linking the frontal operculum to the neural structures known to mediate erection? To our knowledge, such a potential pathway might be the efference from the frontal operculum to the insula (Augustine, 1996; Mufson and Mesulam, 1982), a region where the BOLD signal was found correlated with the penile response in three previous investigations (Arnou et al., 2002; Ferretti et al., 2005; Moulier et al., 2006) and in the present study. The insula, in turn, sends efferents to the medial dorsal nucleus of the thalamus (Augustine, 1996), the ventral striatum (Chikama et al., 1997) and to the cingulate gyrus (Mufson and Mesulam, 1982), regions that have been implicated in the control of erectile responses (Liu et al., 1998; Steers, 2000). However, as correlation is not causation, the correlation between the

insular BOLD signal and the erectile response only suggests that the insula could belong to brain regions that mediate visually induced erections. A similar relaying function has been ascribed to the insula in the domain of emotion: according to Carr et al. (2003), the insula plays a fundamental role in relaying action representation information from the mirror-neuron system to limbic areas processing emotional content, such as the amygdalas, so that the person viewing emotional facial expressions can experience empathy.

Bilaterally, in the inferior parietal lobules (BA 40), where parietal mirror neurons are found (Fogassi et al., 2005), the BOLD signal was significantly correlated with the VPP signal recorded both simultaneously and 20s later. The left inferior parietal lobule (Decety et al., 1994) or both inferior parietal lobules (Stephan et al., 1995) were activated by motor imagery tasks where subjects imagined they were performing movements with their right hand. Similarly, the left supramarginal gyrus (BA 40), where we found the BOLD signal correlated with the plethysmographic measure, was found activated in action observation and in motor imagery tasks (Buccino et al., 2001; Grezes and Decety, 2001; Hanakawa et al., 2003; Stephan et al., 1995). In monkeys, the part of the above mentioned ventral premotor area (F5) containing mirror neurons constitutes a circuit with parietal area PF (Rizzolatti and Arbib, 1998), and PF is thought to correspond to the supramarginal gyrus in humans (Grezes and Decety, 2001). This suggests that the BOLD signal intensity in the inferior parietal lobules and in the left supramarginal gyrus was related to action observation and/or to motor imagery reported by subjects.

The observed correlation between the BOLD signal and the VPP response as well as the dependence of the mirror neuron responses on the level of hunger (Cheng et al., 2006) seem to contradict the report that mirror neurons' responses are not influenced by the motivational significance of the object (Rizzolatti and Craighero, 2004). However, as again correlation is not causation, finding a correlation between the activation of the mirror-neuron system areas and the subsequently recorded erectile response does not suffice to demonstrate that the activation of the mirror-neuron system induces erection. Such correlation might also arise from the fact that brain areas involved in processing VSS could effect both an activation of the mirror-neuron system and an erectile response, with no causal link between the former and the latter effects. In addition, the response of the mirror-neuron system areas could also be related to activity of neurons present in these areas but that are not mirror neurons.

For the lower parts of BA 2, where the BOLD signal was found correlated with penile erection, the highest values of the Z statistic were observed in analyses where the BOLD signal preceded the plethysmographic response (positive lags). By contrast, for negative lags, Z values were consistently equal to zero. This pattern of results does not suggest that this part of the somatosensory cortex responds to inputs from the penis, which is not surprising as the lower part of BA 2 does not correspond somatotopically to the penis. Instead, these findings suggest that activity in the lower part of the somatosensory cortex precede the penile response.

Finally, regions correlated with the VPP response corresponded to the somatotopic representation of the penis in the somatosensory cortex. The VPP response predicted the BOLD signal in the paracentral lobules, a region of the somatosensory cortex reported as corresponding to the penis (Makela et al., 2003; Moulier et al., 2006). Interestingly, the Z-profiles for the

location described as the penile representation in the secondary somatosensory cortex (Kell et al., 2005; Makela et al., 2003; Redouté et al., 2000) showed two maxima, one for a positive lag ("erection precedes BOLD") and one for a negative lag ("BOLD signal in penile somatosensory cortex precedes erection"), which suggests a positive feedback originating from erectile sensations. That the penile response predicts the BOLD signal recorded a few seconds later in the primary sensory cortex corresponding to the penis replicates findings reported in a similar experiment based on the presentation of photographic stimuli (Moulier et al., 2006). The findings of the present study show that the magnitude of penile erection precedes with a lag of 10s to 20s the BOLD signal recorded from the paracentral lobules, cortical somatosensory areas corresponding to the penis. The BOLD signal in the uppermost part of the right lateral somatosensory cortex, another location reported as a somatosensory representation of the penis (Bradley et al., 1998; Redouté et al., 2000; Kell et al., 2005), was correlated with the VPP but the level of the correlation ($p < 0.001$, uncorrected) fell short of the threshold of statistical significance of the present study ($p < 0.05$, corrected).

In conclusion, the theory of the perception-action coupling mechanism based on mirror neurons has previously been expanded to the domain of emotion and to account (at least partly) for emotion processing and empathy (Preston and de Waal, 2002). Thus, observing fearful body expressions not only produces increased activity in brain areas associated with emotional processes but also in areas linked with representation of action and movement (De Gelder et al., 2004). Such a system prompts the observer to resonate with the emotional state of another individual, with the observer activating the motor representations and associated autonomic and somatic responses that stem from the observed target (Preston and de Waal, 2002). Here, we suggest that a similar perception-action coupling mechanism mediated by the mirror-neuron system prompts the observers to resonate with the motivational state of other individuals appearing in visual depictions of sexual interactions, with observers activating motor representations and erectile responses associated with the observed depictions.

Acknowledgments

This work was supported by grants from the French Ministry of Health and from the French Ministry of Research (ACI Cognitive 2001). We thank J.P. Souteyrand (Inserm U742) for his technical assistance.

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Electronic supplementary material - Table 1. Areas where the BOLD signal was correlated positively with the plethysmographic signal

Brain area	BA	Non lagged signal		Lagged signal	
		Left hemisphere	Right hemisphere	Left hemisphere	Right hemisphere
<u>Cortical structures</u>					
Superior frontal gyrus	6	~	/	18 9 60 (4.83)	-18 -9 60 (5.66) / 18 -9 66 (6.20)
	8	-12 24 45 (5.25)	/	~	~ / ~
	9	~	/	39 33 36 (5.65)	~ / ~
Medial frontal gyrus	6	~	/	6 -6 60 (4.81)	~ / 9 -9 63 (4.56)
	8	~		~	-9 39 45 (4.75) / ~
	9	0 30 36 (6.70)	/	~	~ / ~
Middle frontal gyrus	6	~	/	27 6 63 (5.34)	-30 0 51 (5.60) / 33 0 48 (5.42)
	8	~	/	36 30 48 (4.97)	~ / ~
	9	-30 36 36 (5.61)	/	39 33 36 (5.65)	~ / 39 9 30 (4.75)
	10	~	/	42 48 12 (7.08)	~ / 42 48 12 (5.13)
Inferior frontal gyrus					
	46	~	/	~	~ / 48 39 3 (5.25)
	47	-30 24 -15 (3.86)	/	36 24 -15 (5.88)	~ / ~
	44	~	/	54 9 0 (7.84)	-51 12 15 (5.48) / 39 9 30 (4.75)
Precentral gyrus		~	/	48 3 0 (6.15)	~ / ~
	4	~	/	~	-48 3 3 (6.08) / 57 9 39 (5.78)
	6	~	/	63 6 18 (7.30)	~ / ~
Anterior cingulate gyrus	24	-3 -9 33 (5.67)	/	3 12 33 (5.63)	~ / 3 9 30 (5.29)
	25	~	/	~	0 15 -6 (5.59) / ~
	32	0 33 21 (6.82)	/	12 45 6 (6.16)	~ / ~
Cingulate sulcus	31	-15 -30 36 (4.77)	/	~	~ / ~
	32	-33 -18 15 (5.13)	/	~	~ / ~
Posterior cingulate gyrus	23	~	/	18 -54 18 (5.42)	~ / ~
	31	-15 -30 36 (4.77)	/	9 -30 39 (5.30)	~ / ~
Postcentral gyrus	1	~	/	~	~ / 51 -27 57 (5.62)

	2	~	/	~	-60 -21 27 (7.84)	/	60 -24 24 (7.33)
	3	~	/	~	~	/	60 -12 21 (4.95)
	3	~	/	~	~	/	60 -12 21 (4.95)
	40	-51 -27 21 (5.26)	/	~	~	/	~
	43	-54 -18 21 (5.82)	/	66 -12 21 (5.68)	~	/	~
Superior parietal lobule	7	~	/	~	-21 -60 45 (5.76)	/	33 -45 66 (7.28)
Postcentral sulcus	40	~	/	~	~	/	36 39 69 (7.27)
		~	/	~	-51 -33 48 (6.05)	/	57 -27 48 (6.02)
Inferior parietal lobule	40	-60 -27 21 (6.37)	/	57 -39 51 (7.09)	~	/	~
Supramarginal gyrus	40	-54 -45 33 (5.77)	/	~	~	/	~
Insula						/	
		-42 3 6 (7.75)	-				
Anterior insula		33 18 0 (6.41)	/	~	-39 12 -9 (5.19)	/	42 6 -6 (5.57)
Posterior insula		~	/	42 -12 3 (5.48)	-42 -6 -6 (4.95)	/	42 0 9 (6.10)
Transverse temporal gyrus	42	~	/	63 -18 12 (5.76)	~	/	~
Superior temporal gyrus	22	-54 -3 0 (5.12)	/	60 -6 0 (7.04)	~	/	57 -9 0 (5.58)
	37	~	/	~	-51 -57 -3 (5.98)	/	51 -63 -6 (6.76)
	38	~	/	48 15 -9 (7.07)	~	/	~
	42	~	/	60 -33 12 (4.78)	~	/	~
Inferior temporal gyrus	37	~	/	~	~	/	51 -63 -6 (6.76)
Hippocampe		~	/	~	-36 -39 -3 (7.06)	/	~
Parahippocampal gyrus	30	~	/	~	-18 -36 3 (4.98)	/	~
Fusiform gyrus	37	~	/	~	-36 -60 -12 (5.67)	/	~
Cuneus	18	~	/	6 -78 21 (4.96)	~	/	~
Precuneus	7	-9 -66 39 (4.76)	/	15 -51 51 (4.79)	~	/	21 -72 39 (4.73)
Precuneus	31	~	/	15 -63 30 (6.24)	~	/	~
Middle occipital gyrus	19	~	/	~	~	/	42 -78 -6 (7.82)
Lingual gyrus	18	~	/	~	~	/	15 -81 -3 (5.23)
Parietooccipital sulcus	18	~	/	~	~	/	~
<u>Subcortical areas</u>							
Thalamus		~	/	15 -9 12 (5.53)	~	/	12 -6 12 (5.00)

Caudate nucleus	~	/	18 21 -6 (5.44)	-21 -6 24 (6.17)	/	21 -27 18 (7.40)
Putamen	~	/	27 3 -9 (5.43)	~	/	~
Clastrum	-36 -12 -6 (5.97)	/	33 3 9 (5.40)	-33 0 12 (4.96)	/	~

Others

Cerebellum	~	/	6 -51 -21 (5.27)	~	/	~
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Electronic supplementary material - Table 2. Areas where the BOLD signal was correlated negatively with the plethysmographic signal

Brain area	BA	Non lagged signal			Lagged signal		
		Left H.		Right H.	Left H.		Right H.
Superior frontal gyrus	10	~	/	~	~	/	18 60 24 (6.41)
	8	~	/	~	~	/	9 33 57 (4.98)
Medial frontal gyrus	6	~	/	~	-9 12 51 (5.56)	/	~
Inferior frontal gyrus	44	~	/	~	~	/	51 18 9 (5.68)
	47	~	/	~	-48 27 -3 (5.22)	/	~
Inferior parietal lobule	40	~	/	~	~	/	48 -66 45 (4.73)
Anterior cingulate gyrus	32	~	/	~	-9 36 33 (5.40)	/	~
Posterior cingulate gyrus	30	3 -48 18 (4.81)	/	~	~	/	~
	26	~	/	~	~	/	6 -48 12 (5.49)
Angular gyrus	39	~	/	~	-42 -72 36 (5.31)	/	~
Supramarginal gyrus	40	~	/	~	-57 -57 27 (5.73)	/	60 -57 36 (6.46)
Middle temporal gyrus	21	~	/	~	~	/	60 -33 0 (5.61)
	22	~	/	~	-57 -39 0 (5.90)	/	~
Postcentral gyrus	40	-45 -12 21 (4.74)	/	~	~	/	~
Precuneus	31	-24 -63 21 (4.98)	/	~	~	/	~

Notes: see Electronic supplementary material - Table 1.

Electronic supplementary material - Table 3. Areas activated by the presentation of visual sexual stimuli

Brain area	BA	BLOCK+		ONSET+	
		Left hemisphere	Right hemisphere	Left hemisphere	Right hemisphere
<u>Cortical structures</u>					
Superior frontal gyrus	6	~	/	~	-24 -3 69 (4.79) / ~
Middle frontal gyrus	6	~	/	~	-30 -9 60 (5.50) / 30 -6 57 (4.94)
Inferior frontal gyrus	9	~	/	~	~ / 45 9 24 (4.91)
Anterior cingulate gyrus	24	~	/	~	~ / 0 3 33 (4.73)
Superior parietal lobule	7	~	/	~	-33 -51 51 (6.32) / 33 -51 60 (6.31)
Inferior parietal lobule	40	~	/	~	-39 -45 57 (6.10) / ~
Insula		~	/	~	-30 15 6 (3.39) / ~
Inferior temporal gyrus	19	~		~	~ / 48 -63 -6 (5.19)
	37	-48 -69 -3 (5.17)	/	~	~ / ~
Middle temporal gyrus	39	~		~	~ / 48 -60 9 (5.03)
Fusiform gyrus	37	-39 -45 -15 (5.43)	/ 45 -57 -18 (5.24)	~	/ ~
Precuneus	7	~	/	~	-24 -57 51 (5.66) / ~
	19	~	/	~	-21 -75 33 (5.01) / 30 -81 33 (5.42)
Inferior occipital gyrus	19	~	/ 45 -72 -9 (6.37)	~	/ ~
Parahippocampal gyrus	27	~	/	~	-9 -36 -6 (4.52) / ~
<u>Subcortical structures</u>					
Thalamus		~	/	~	-6 -6 9 (4.83) / ~
Striatum		~	/	~	-6 9 -3 (3.92) / ~
<u>Others</u>					
Cerebellum		~	/	~	~ / 3 -48 -3 (4.41)