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Differential cerebral activation during observation of expressive gestures and motor acts

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Abstract

We compared brain activation involved in the observation of isolated right hand movements (e.g. twisting a lid), body-referred movements (e.g. brushing teeth) and expressive gestures (e.g. threatening) in 20 healthy subjects by using functional magnetic resonance imaging (fMRI). Perception-related areas in the occipital and inferior temporal lobe but also the mirror neuron system in the lateral frontal (ventral premotor cortex and BA 44) and superior parietal lobe were active during all three conditions. Observation of body-referred compared to common hand actions induced increased activity in the bilateral posterior superior temporal sulcus (STS), the left temporo-parietal lobe and left BA 45. Expressive gestures involved additional areas related to social perception (bilateral STS, temporal poles, medial prefrontal lobe), emotional processing (bilateral amygdala, bilateral ventrolateral prefrontal cortex (VLPFC), speech and language processing (Broca's and Wernicke's areas) and the pre-supplementary motor area (pre-SMA). In comparison to body-referred actions, expressive gestures evoked additional activity only in the left VLPFC (BA 47). The valence-ratings for expressive gestures correlated significantly with activation intensity in the VLPFC during expressive gesture observation. Valence-ratings for negative expressive gestures correlated with right STS-activity. Our data suggest that both, the VLPFC and the STS are coding for differential emotional valence during the observation of expressive gestures.

Keywords: Gesture; Emotion; Social interaction; Mirror neurons; STS; BA 47

1. Introduction

Several studies in monkeys, descriptions of deficits of patients with circumscribed lesions and functional imaging studies have been performed on the topic of gesture observation and recognition. These studies demonstrated that differential brain areas are active during observation of specific aspects of meaningful gestures. However, different types of hand gestures within the same pool of subjects were so far not assessed. On the basis of previous studies we selected three types of meaningful gestures: isolated hand movements, body-referred hand movements and expressive gestures performed with one hand. In order to compare cerebral activation during the observation of these three gesture types we used functional magnetic resonance imaging (fMRI) during gesture observation in 20 healthy subjects.

The perception of gestures in contrast to other objects presented is distinct already at the level of the occipito-temporal junction (Peigneux et al., 2000). In monkeys, Mishkin and Ungerleider (1982) differentiated a ventral pathway, related to object recognition (face and form; via V3 and inferior parietal), and a dorsal pathway for visual guidance of actions towards objects (movement; via V5 and superior parietal). During observation of hand actions monkeys show increased activation in the dorsal pathway (Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995). Neurons mirroring hand movements are located in F5 ("mirror neurons": di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti,

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1992; Rizzolatti & Arbib, 1998; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996). The human homologue to F5 is probably BA 44 within the pars opercularis of the inferior frontal gyrus (Rizzolatti, Fogassi, & Gallese, 2002) overlapping with the ventral premotor cortex (PMC; lateral BA 6). Patients with lesions in BA 44 and BA 6 failed to show deficits in movement imitation and observation (Haaland, Harrington, & Knight, 2000)—probably because this ability is represented bilaterally (Muhlau et al., 2005). Although the pars opercularis of the left inferior frontal gyrus and the adjacent premotor cortex are predominantly active during imitation of movements (Buccino et al., 2004; Grezes, Armony, Rowe, & Passingham, 2003; Heiser, Iacoboni, Maeda, Marcus, & Mazziotta, 2003; Iacoboni et al., 1999) and especially during target-directed movements (Koski et al., 2003), this area is also active during observation of hand (Binkofski et al., 1999a, 1999b; Nishitani & Hari, 2000) and body movements (Buccino et al., 2001). Additional areas related to language production and perception – such as Broca's and Wernicke's area – have been demonstrated to be active if meaningful common hand movements were compared with meaningless ones (Decety et al., 1997).

Mirror neurons might not be restricted to the frontal lobe since they have also been described in the inferior parietal gyrus (Fogassi et al., 2005; Rizzolatti, Fogassi, & Gallese, 2001). These mirror neurons inferior to the parietal sulcus might allow the monkey to understand the intentions of the actor of the observed movements.

Humans with parietal lesions often present symptoms of apraxia. Ideational and ideomotor apraxias represent supramodal apraxias, i.e. the disturbed motor behavior is not restricted to a particular modality but affects the ideation, and conception of the intended motor acts at a global level. These most complex forms of apraxia have been associated with lesions of the supramarginal or angular gyrus (Freund, 1992).

During movement imitation these patients show predominantly deficits for body-referred hand movements but less for isolated hand gestures (Goldenberg, 1995; Halsband et al., 2001).

Original models of apraxia have already described that these patients display not only production deficits but also deficits in gesture perception (Roy & Square, 1985) and other studies support this opinion (Goldenberg, 1999).

Both, the dorsal pathway and ventral pathway terminate in a common polysensory area, the superior temporal sulcus (STS), where the perception of form and motion interact (Oram & Perrett, 1996; Vaina, Solomon, Chowdhury, Sinha, & Belliveau, 2001). This area might be responsible for the matching of an observed movement with a stored motor representation (Iacoboni et al., 2001). In the STS, both facial and hand movements are analyzed according to their social significance (Allison, Puce, & McCarthy, 2000). The STS is part of the so-called "theory of mind" areas (Frith & Frith, 1999), additionally consisting of the dorsal PMC and the temporal poles (Gallagher & Frith, 2003; Vogeley et al., 2001) and is active during setting oneself into another's perspective ("mentalizing"). It has been shown that these areas are involved in the perception of expressive gestures (Gallagher & Frith, 2004).

In comparison to body-referred movements expressive gestures are usually associated with emotional responses predominantly expressed via facial characteristics. The medial part of the ventral PFC is involved in the active analysis and evaluation of the emotional valence of pictures and facial expressions (e.g. Phan et al., 2004). In contrast, the VLPFC might be more associated with the passive perception of emotional stimuli (facial expressions: Blair, Morris, Frith, Perrett, & Dolan, 1999; perception of emotional intonation: Wildgruber et al., 2004). This area has recently been described as an area important for the feelings of sadness after the presentation of sad films in adults (Levesque et al., 2003) and children (Levesque et al., 2004). Additionally, expressive gestures are not only used for emotional interaction but also for neutral information which carry a semantic content. In contrast to body-referred movements this content is performed to interact with another subject and its semantic component has to be decoded—comparable to sign language recognition (Goldin-Meadow, 1999).

We hypothesized that observation of all three type of movements (isolated hand movements, body-referred movements and expressive gestures) might be associated with activation in the ventral and the dorsal pathway including the frontal and parietal "mirror neurons".

The inferior parietal lobe was expected to be more involved during observation of body-referred movements than of isolated hand movements, since patients with lesions in this area show higher deficits in imitation of body-referred compared to isolated hand movements. The involvement of the STS should be increased when more socially relevant objects are observed. Therefore, body-referred movements should elicit more STS-activation than isolated hand movements. Additionally, we hypothesized that activation of Broca's and Wernicke's areas might be enhanced during observation of expressive gestures being highly communicative in its purpose. Finally, we hypothesized that the increasing emotional content of expressive gestures might result in increased activation of areas processing emotions. In a correlation analysis we tested the possible correlation of valence ratings of the expressive gestures with BOLD effect magnitude in regions of interest. Most reasonable candidates would be the amygdala, important for facial expression observation (Blair et al., 1999; Breiter et al., 1996; Hariri et al., 2000; Iidaka et al., 2001), the VLPFC and the adjacent pars opercularis of the inferior frontal gyrus which has been shown to be involved in passive perception of emotional stimuli in different modalities and the STS which is highly important for processing of social relevant stimuli.

2. Methods

2.1. Subjects

Twenty volunteers (mean age 52.30 years; S.D. = 12.40; range: 22–69 years; 10 male) without history of neurological or psychiatric disease were recruited by announcements at the University and a local adult education center. All participants were right handed (lateralization quotient for the right side of more than 90%) as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971). The study was approved by the Ethics Committee of the Medical Faculty of the University of Tübingen. Written informed

Fig. 1. Description and illustration of the video material presented.

consent was obtained according to the guidelines of the Declaration of Helsinki.

2.2. Task and material

The volunteers participated in an fMRI examination during the observation of various meaningful gestures and motor acts (see Fig. 1): isolated hand movements of the right dominant hand (12 video clips without presentation of the face and the body of the actor), body-referred movements (12 video clips) and expressive gestures (18 video clips with 6 emotionally neutral, 6 negatively and 6 positively rated gestures). Clips with expressive gestures and body-referred movements presented hand movements together with the actor's face and upper half of the body. Isolated hand movements and body-referred movements were divided into movements with objects and identical movements without objects to control for possible differences between the recognition of movements and of movement-related objects. Expressive gestures, without articulation (Zinober & Martlew, 1985), included changes in facial expression, body postures as well as hand actions. The duration of each video was 3 s, the frame rate 30 pictures per second. A grey field with the averaged luminance of all clips and the same size as the videos was shown between the presentation of the video-clips (baseline). Subjects were told to keep their eyes open and look at the screen shown on a mirror attached to the head coil via a video projector. They were instructed not to imitate the presented movements. Subjects showed no visible movements of their hands during gesture presentation. This was controlled by both visual inspection and video-control from the back of the fMRI-tunnel.

The video material was validated for its emotional valence and meaning by 10 healthy subjects who did not participate in the fMRI study (reference group, mean age 31.70 years; S.D. = 5.98; range: 24–43 years). They rated the emotional valence of expressive gestures with a visual analogue scale (VAS) ranging from emotional negative (−5), neutral (middle, 0) to emotional positive (+5). There was no significant difference in the recognition of the different movement categories. In the validation group 97.8% of the expressive gestures, 96.4% of the pantomimed and 100% of the movements with objects were correctly recognized on the video material. The three groups of expressive gestures were different with respect to emotional valence (negative: −3.70 (S.D.: 1.31), neutral: −0.12 (S.D.: 1.65), positive 2.20 (S.D.: 2.56); MANOVA: $F(2,36) = 151.47$; $p < 0.001$).

Subjects were asked to imagine themselves in the position of the addressee during the observation of expressive gestures. Execution of any movement during gesture observation was discouraged. This was controlled by video observation during scanning. After the fMRI-measurements, the subjects evaluated the observed gestures and hand movements in the same manner as the reference group.

2.3. fMRI

Whole head scans were performed with a 1.5 T whole body Scanner (Siemens Vision) using echo planar imaging (EPI; TE: 40 ms; TR: 3 s, 28 axial slices of 4 mm slice thickness and 1 mm gap, matrix 64 × 64; Klose, Erb, Wildgruber, Muller, & Grodd, 1999). In an event-related design, the 42 different video clips, each lasting 3 s, were presented in a pseudo-randomized order, each clip appearing twice (6 whole brain scans per clip adding to 42 × 2 × 6 = 504 EPI data sets per subject). The intersession interval (ISI) was 18 s in order to enable both a modulation of the main effects of each type of gesture and differences between gesture types.

The first three EPI data sets of each session were discarded prior to analysis to allow for T1-saturation effects. Data were analyzed with the statistical parametric mapping program (SPM99, Wellcome Department of Imaging Neuroscience) running on Matlab version 5.3.1 (MathWorks Inc; Natick, MA; USA). Each individual scan was realigned to the first one of each scanning condition to correct for movement artefacts. The realigned data were spatially normalized to the MNI-template and resliced with 3 mm × 3 mm × 3 mm. The resulting images were smoothed with a 9 mm (full width at half maximum) Gaussian filter. Individual statistical maps (fixed effect) were calculated for each type of gesture (main effect) and for interactions between different types of gestures. Since the ISI was quite long we did not use jittering. Contrasts for each condition and differences between conditions were calculated for each subject. Contrast images of each subject were then used for group statistics calculated as random effects analysis at the 2nd level, which takes variance between subjects into account. The statistical threshold used to report group-activations was set as $p < 0.05$ corrected for the whole brain (false discovery rate; FDR; Genovese, Lazar, & Nichols, 2002). Activation sites over $t = 5.40$ fulfilled FWE-criteria (family wise error; Brown & Russell, 1997). t-values of significant activations of the highest activated voxels were given for the MNI-coordinates and were assigned to anatomical regions. All regions were detected with the "Automated Anatomical Labelling" software (AAL; Tzourio-Mazoyer et al., 2002). In the correlation analysis we corrected for multiple comparisons between regions of interest (ROIs; $n = 4$: amygdala, VLPFC, pars opercularis of the inferior frontal gyrus and STS,), for the two hemispheres ($n = 2$) and three emotionally different types of expressive gestures (negative, neutral and positive). A statistical threshold of $p < 0.05$ must therefore be divided through 4 × 2 × 3 which results in a corrected p-value of $p < 0.002$.

Corrected *p*-values given for the correlation analysis were therefore multiplied with 24. We plotted parameter estimates of the highest activated voxel within two ROIs for each subject during observation of expressive gestures together with the individual ratings.

3. Results

3.1. Rating of video-clips

The participants did not differ in the recognition of presented gestures (average of number of errors 2.65; Mann–Whitney *U*-test: $z = 1.81$; n.s.) and the emotional valence of expressive gestures (negative average: −3.23; positive average: 2.37; n.s.; range: −5 to 5) in comparison to the reference group.

3.2. fMRI-effects for all stimuli

All types of gestures induced activation in the bilateral occipito-temporal junction including V3, V5 and face recognition areas in the inferior temporal lobe (fusiform gyrus; see Supplementary Tables 1–3 and Fig. 2). In addition, the right ventral PMC reaching into the opercular and triangular gyrus (BA 44) and the superior bank of the anterior intraparietal sulcus (BA 7) were activated during all conditions.

3.3. Effects of isolated hand movements

Observation of isolated hand movements revealed no specific activation site, which was not shared by the other two conditions (see Fig. 2).

3.4. Effects of body-referred movements

Observation of body-referred movements compared to movements performed with an isolated hand induced increased activity in the bilateral posterior STS together with the adjacent posterior superior temporal gyrus, angular and supramarginal gyrus (Table 1; Fig. 3A). Additionally the right triangular part (BA 45) of the inferior frontal gyrus showed higher activation than during observation of isolated hand movements.

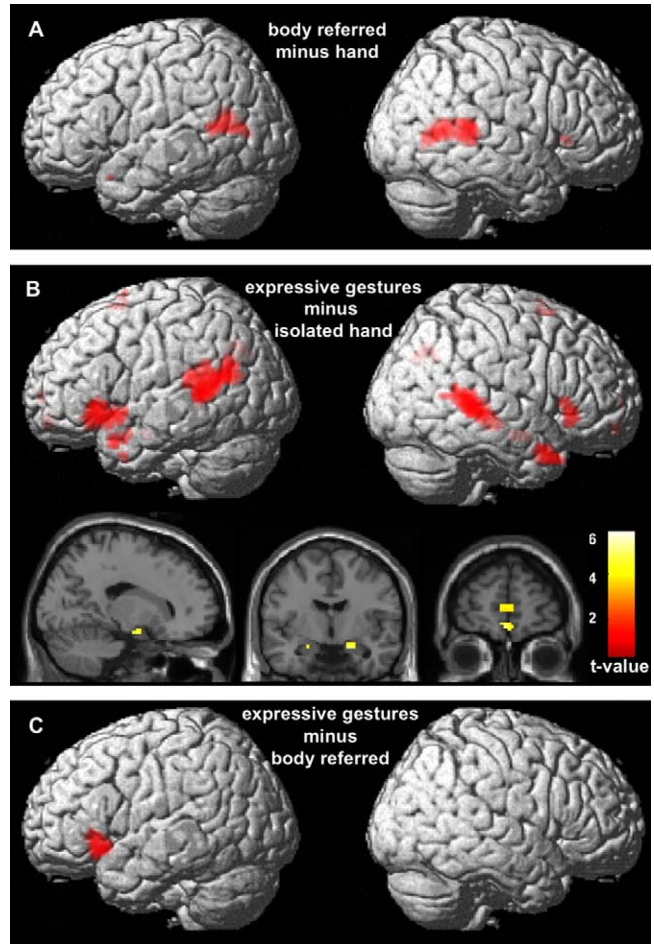

Fig. 3. Differences between the three types of gestures: (A) body-referred minus isolated hand movements; (B) expressive gestures minus isolated hand movements; (C) expressive gestures minus body-referred movements.

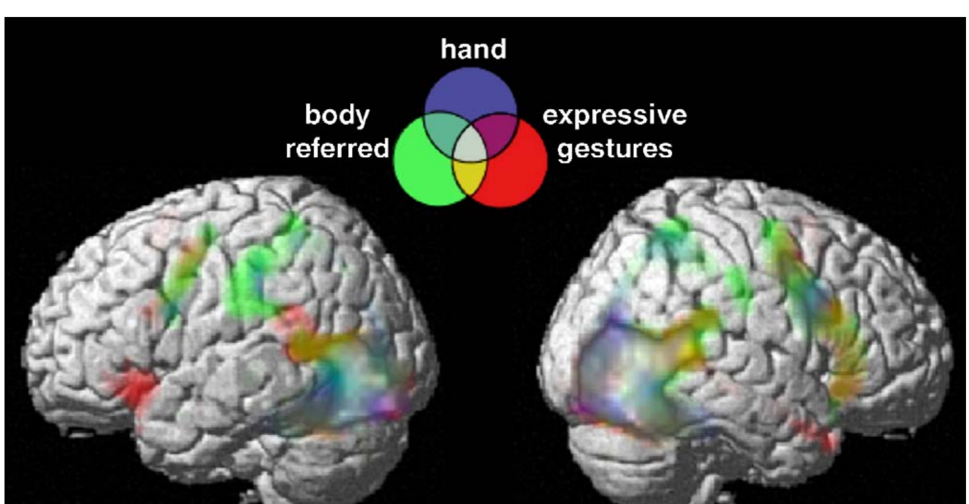

Fig. 2. Main effects for all types of gestures projected on the SPM render brain and overlayed colour coded for each type of gesture. Isolated hand actions (blue), body-referred actions (green), expressive gestures (red). Overlay is coded in additive colouring demonstrated with colour circles.

Table 1
Body-referred minus isolated hand movements

Area (Brodmann's area)	*p*-value	*t*-value	MNI-coordinates (*x*, *y*, *z*)		
Differential effect *t*-tests (corrected for entire volume with $p<0.05$; FDR)					
Posterior STS le	0.011	6.98	−48	−57	15
Posterior STS ri	0.011	6.55	54	−57	9
	0.014	5.49	60	−39	3
Inf. frontal triangular ri (BA 45)	0.016	4.90	57	27	3
Angular gyrus le (BA 40)	0.025	4.42	−45	−60	24
Temporal planum le (BA42)	0.03	4.24	−60	−48	12
Supramarginal gyrus le (BA 40)	0.04	4.00	−51	−21	33

3.5. Effects between pantomimed movements and movements with objects

No differential activation was observed when movements with and without objects were compared.

3.6. Effects for expressive gestures

Expressive gesture observation compared to those of isolated hand movements elicited increased activity in the bilateral STS and superior temporal gyrus, bilateral temporal pole, medial PFC (BA 10), left supramarginal and angular gyrus (BA 40), bilateral inferior frontal gyrus (triangular inferior part; BA 45), bilateral VLPFC (BA 47), bilateral amygdalae, pre-SMA and lingual gyrus (Table 2, Fig. 3B).

In comparison to body-referred gestures, a condition in which also the face, the trunk and the upper extremities of the performer were shown, only the left VLPFC (BA 47) showed significant increase of activation (Table 3, Fig. 3C).

3.7. Correlation of BOLD-magnitude with emotional valence

The right STS showed a significant positive correlation with valence ratings for negative gestures (coordinates: 54, −36, 6; $r=0.78$; $t(18)=5.30$; pcorr = 0.001; see Fig. 4A). Correlation analysis between the absolute valence rating of all expressive gestures and the activation in preselected ROIS (STS, opercular gyrus, VLPFC, amygdala) revealed a significant positive correlation within the VLPFC left (coordinates: −51, 21, −12; $r=0.44$; $t(58)=3.74$; pcorr = 0.002; see Fig. 4B).

4. Discussion

In this study we investigated all three types of gestures (isolated hand movements, body-referred movements and expressive gestures) in the same group of healthy subjects. Comparison between activation maps obtained during observation of isolated hand movements, body-referred movements and expressive gestures revealed differences between these types of gestures. Differences emerged especially in areas associated with social perception and emotional valence.

4.1. Shared activation sites during observation of all type of movements

The observation of all types of gestures evoked activation in visual perception areas of the occipital and occipito-temporal lobe (V3, V4; V5 (cf. Reppas, Niyogi, Dale, Sereno, & Tootell, 1997); frontal eye fields (cf. Gitelman, Parrish, Friston, & Mesulam, 2002); fusiform gyrus (cf. Haxby, Hoffman, & Gobbini, 2000; Shmuelof & Zohary, 2005) the ventral PMC

Table 2
Expressive gestures minus isolated hand movements

Area (Brodmann's area)	*p*-value	*t*-value	MNI-coordinates (*x*, *y*, *z*)		
Differential effect *t*-tests (corrected for entire volume with $p<0.05$; FDR)					
Superior temporal gyrus ri (post STS)	0.001	9.21	54	−39	3
Superior temporal gyrus le (post STS)	0.004	6.11	−66	−45	9
Angular gyrus le (BA 40)	0.001	7.11	−54	−63	24
Post. supramarginal gyrus le (BA 40)	0.014	4.79	−63	−45	24
Temporal planum le (BA42)	0.007	5.43	−60	−45	12
Temporal pole ri (BA38)	0.001	7.04	51	12	−30
Temporal pole le (BA 38)	0.007	5.33	−36	9	−9
Inf. frontal; triangular gyrus ri (BA 45)	0.002	6.46	57	27	−3
Inf. frontal; triangular gyrus le (BA 45)	0.007	5.33	−51	24	−6
VLPFC le (BA 47)	0.004	5.94	−57	12	−9
VLPFC ri (BA 47)	0.005	5.91	54	27	−6
Amygdala ri	0.008	5.22	21	−6	−18
Amygdala le	0.03	3.94	−21	−6	−18
mPFC (BA 10)	0.009	5.06	0	54	−12
Lingual gyrus ri (BA 18)	0.013	4.73	6	−27	−6
Ant. supplementary motor area (BA 6)	0.015	4.58	3	12	63

Table 3
Expressive gestures minus body referred movements

Area (Brodmann's area)	*p*-value	*t*-value	MNI-coordinates (*x*, *y*, *z*)		
Differential effect *t*-tests (cluster corrected for entire volume with $p<0.05$; FWE)					
VLPFC le (BA 47)	0.03	5.49	−54	21	−9

(lateral BA 6) and pars opercularis (BA 44) of the inferior frontal gyrus in both hemispheres. This observation confirms previous reports of areas active during observed action of isolated hands in humans (Binkofski et al., 1999a, 1999b; Decety et al., 1997; Molnar-Szakacs, Iacoboni, Koski, & Mazziotta, 2005; Nishitani & Hari, 2000). Therefore, all gestures presented involve the "dorsal pathway" including the anterior intraparietal sulcus (Shmuelof & Zohary, 2005). Consistent with the findings of Zentgraf et al. (2005) expressive gesture observation also involved the pre-SMA. In our study no significant difference was seen when activation maps during observation of movements with and without tools were compared. Nevertheless, studies in apraxic patients showed differences in the recognition of gestures performed with and without tools (Goldenberg & Hagmann, 1998).

4.2. The parietal lobe and apraxia

Interestingly, all gestures elicited activation in the inferior parietal gyrus, an area that is part of the dorsal pathway

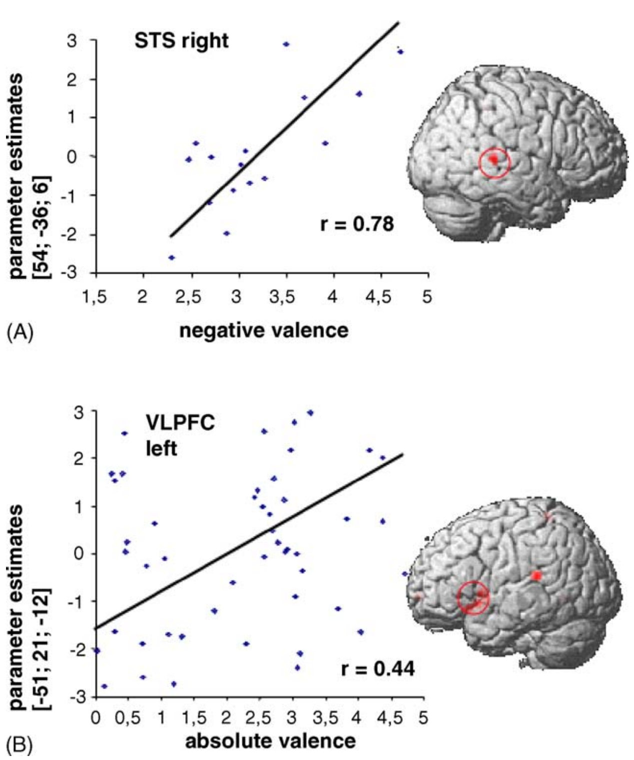

Fig. 4. (A) BOLD-intensity within the right STS during negative expressive gesture observation correlated significantly with negative valence rating of expressive gestures observed ($r=0.78$). (B) BOLD-intensity within the left VLPFC during observation of all expressive gestures (three data-points per subject) correlated significantly with absolute valence rating of expressive gestures observed ($r=0.44$).

(Shmuelof & Zohary, 2005) and of the mirror neuron system (Fogassi et al., 2005; Rizzolatti et al., 2001) and might be important for associating movement with its context. The inferior part of BA 40 was active during body-referred movements but not during movements of isolated hands, and the statistical comparison between both conditions revealed differential activation in BA 40. This finding was previously described during observation of meaningless gestures (Hermsdörfer et al., 2001).

In apraxia lesions are not restricted to the parietal lobe but often comprise parts of the STS—an area which showed bilaterally increased activation during body-referred movements in comparison to isolated hand movements. Thus, the bilateral STS may be crucial for the *recognition* of body-referred movements in a social context, while the inferior left parietal lobe appears to be more involved in the *production* of movements in reference to the body.

4.3. STS

Observation of body-referred compared to hand gestures induced increased activity in the bilateral posterior STS—a location which is consistent with findings of observations of body movements from other studies (Bonda, Petrides, Ostry, & Evans, 1996; for an overview see Allison et al., 2000). The higher the social relevance and the more aspects of observed body parts are involved in a movement, the higher the activation in the STS bilaterally. Whereas observation of body movements is represented in a more posterior region, observation of movements of the eyes and the mouth are represented in the anterior STS (for a review see Allison et al., 2000). Therefore, activation observed during expressive gestures was located anterior compared to that during observation of isolated hands or hands in reference to the body. This area of the STS may have an integrative function for the processing of socially relevant signals irrespective of modality (e.g. visual or auditory: Barraclough, Xiao, Baker, Oram, & Perrett, 2005). It has been demonstrated in the monkey that the STS does not code facial recognition but for recognition of the social-interactive relevance of the observed facial expression (Heywood & Cowey, 1992). Our data on observation of expressive gestures in humans are in accordance with these findings: the activity in the right STS correlated only for the negative but not for the valence of observed expressive gestures in general.

Nakamura et al. (1999) also highlighted the importance of the right STS for attention to facial emotion. Gallagher and Frith (2004) concluded that the right STS is sensitive to stimuli that signal the actions of another individual. The social relevance of a negative emotional stimulus may indicate an anticipated aggressive action.

4.4. BA 47, emotional processing and the semantic context

The left VLPFC was significantly more active during observation of expressive gestures compared to body-referred movements. It has been demonstrated before that BA 47 is associated with the passive perception of visual (faces: Blair et al., 1999; Levesque et al., 2003) and linguistic (Wildgruber et al., 2004) emotional stimuli. BA 47 is also active during processes of recognition and evaluation (right hemispheric: emotional identification of prosody—Wildgruber et al., 2005; left hemispheric: recognizing versus observing videos of expressive gestures—Gallagher & Frith, 2004). Our subjects were given an instruction to passively observe the expressive gestures and take a role as the addressee for the gestures presented. BA 47 is thought to reflect the individual's attempts to regulate the emotion evoked by the stimuli (Elliott, Dolan, & Frith, 2000; Phillips et al., 2001). In the present study the VLPFC correlated significantly with the valence ratings of all expressive gestures and might therefore be important for the coding of the valence of all emotional qualities of expressive gestures. Recently, this area has been described to be associated with the feeling of sadness after presentation of sad films in adults (Levesque et al., 2003) and children (Levesque et al., 2004).

Not only the emotional but also the increased semantic aspect might to be processed in BA 47 (see also Dapretto & Bookheimer, 1999). An involvement in semantic processing has repeatedly been reported for the left VLPFC (e.g. Fiez, 1997). Together with an increase of activation within the left triangular gyrus – in comparison to isolated hand movements – our data point to increased semantic processing during expressive gesture observation and to parallels in the perception of expressive gestures and language.

4.5. Limitations of the study

This study has several limitations. In order to balance effects of pantomimed movements and movements with tools we presented both types during the isolated and the body-referred movements. Since expressive gestures were performed without tools this confound might have led to differences between expressive gestures and the other two conditions. However, a direct comparison between activation maps during observation of movements performed with and without tools did not reveal significant differences. Additionally, we did not control for any facial movements during the observation of gestures and can therefore not exclude associated mimic activation. Another point is that the instruction was different for the observation of expressive gestures than for those of the two other conditions which might have influenced the resulting activation maps. All these issues should be considered in a future investigation.

5. Conclusion

We observed different activation sites, which have been described to be involved in emotional and semantic processing, mentalizing and object recognition during the observation of different types of meaningful gestures. Our data point to the importance of the parieto-temporal cortex for the observation of body-referred motor acts. Furthermore, they highlight the importance of areas involved in social interaction and the VLPFC for expressive gesture recognition.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.neuropsychologia.2006.03.016.

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