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NeuroImage

www.elsevier.com/locate/ynimg
NeuroImage xx (2007) xxx–xxx

Perceiving fear in dynamic body expressions

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Received 31 July 2006; revised 16 November 2006; accepted 17 November 2006

Characteristic fear behaviour like putting the hands in front of the face and running for cover provides strong fear signals to observers who may not themselves be aware of any danger. Using event-related functional magnetic resonance imaging (fMRI) in humans, we investigated how such dynamic fear signals from the whole body are perceived. A factorial design allowed us to investigate brain activity induced by viewing bodies, bodily expressions of fear and the role of dynamic information in viewing them. Our critical findings are threefold. We find that viewing neutral and fearful body expressions enhances amygdala activity; moreover actions expressing fear activate the temporal pole and lateral orbital cortex more than neutral actions; and finally differences in activations between static and dynamic bodily expressions were larger for actions expressing fear in the STS and premotor cortex compared to neutral actions.

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Keywords: Emotion; Fear; Bodies; Amygdala; Action representation; fMRI

Introduction

The sound of gunfire immediately causes one to bend forward and to run for cover. Such characteristic fear behaviour protects from danger and also communicates a strong fear signal to observers who may not have heard the noise themselves. Emotional body language (EBL) provides reliable cues to recognise another's emotions even when viewed from a distance and when the facial expression is not visible. The few currently available studies show that EBL can readily be recognised whether in static postures (de Gelder et al., 2004; Sprengelmeyer et al., 1999), whole body movements (Atkinson et al., 2004; Wallbott and Scherer, 1986) or even simple dynamic point-light displays (Dittrich et al., 1996; Bonda et al., 1996). Because of its survival value, the ability to grasp EBL is likely based on

processes that are rapid, highly automatic and possibly relies systems.

At present, very little is known about the neural basis of perceiving EBL. As far as visual communication of emotion is concerned, our most valuable insights are based on investigations using images of static facial expressions. Amygdala and mid-fusiform cortex have consistently been associated with viewing facial expressions of fear (Adolphs, 2002; Dolan, 2002; Haxby et al., 2002). These two brain structures appear also to be important for processing fearful EBL (Hadjikhani and de Gelder, 2003). Yet besides the fact that facial expressions and EBL may share important brain structures, seeing EBL also evokes body specific activations (de Gelder et al., 2004). This is not surprising since EBL represents not only salient visual information but requires that the observer perceives the movements represented in the dynamic images or implied in the still pictures (running away) and grasps the meaning of the action (fleeing from danger).

Some of these characteristic aspects of EBL have recently been addressed in relatively separate research domains. For example, a possible role of premotor areas in emotion recognition has been revealed in brain imaging studies using dynamic facial expressions. Viewing dynamic facial expressions as compared to static ones engages areas processing biological movements and emotion such as the superior temporal sulcus (STS) and the amygdala (AMG), but also areas involved in the production of facial expressions, in particular the parietal and premotor cortex (Decety and Chaminade, 2003; Sato et al., 2004). These results suggest that dynamic images elicit more activity in the areas representing the affective meaning of the stimulus like the amygdala because they provide more information than static ones. On the other hand, dynamic stimuli also contain explicit movement information and this presumably elicits activity in movement sensitive areas like superior temporal sulcus (STS) and in premotor areas, as is indeed the case for dynamical facial expressions (LaBar et al., 2003; Sato et al., 2004). Given the limited information presently available it is unclear whether the different patterns of activation for dynamic and still images reflect a quantitative or also a qualitative difference. In other words, it is not yet clear whether the presence of dynamic

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information makes a substantial difference. It may be difficult to sort this issue out in the case of faces also because movement may be perceived implicitly even when it is not represented explicitly in the stimuli.

As the examples above bring out, we often perceive EBL when watching a person engaged in one or another action, like running away but also opening the door and making angry or fearful gestures at the unexpected visitor. On some occasions the EBL is directly linked with the emotion as in the case of fear and associated flight reaction as in our previous study (de Gelder et al., 2004). In the case envisaged EBL consists of an instrumental action performed with a strong emotional overtone as when we see a hand grasping a glass angrily (Grosbras and Paus, 2006). Thus clarifying how the brain processes EBL raises issues related to action perception which one does not encounter when investigating emotion expressed in the face.

It is now well established that when one observe other people's actions, there is activation in the STS, the parietal and the premotor cortex (see review Grèzes and Decety, 2001). This suggests that action observation automatically triggers action representations. This mechanism of shared representations was proposed as the basis of action recognition (Jeannerod, 2001; Rizzolatti et al., 2001; Gallese et al., 2004; Iacoboni, 2005) but also more recently emotion recognition (Preston and de Waal, 2002; Carr et al., 2003; Gallese et al., 2004). Yet the relation between perceiving the emotion and representing the action has not received much attention so far. Furthermore, research on emotion has predominantly used still faces while investigations of action observation most often used video clips. The few available human neuropsychological findings indicate that the dorsal system may sustain some degree of visual processing of dynamic expression of emotion. For example, patients with focal amygdala lesion are impaired in recognizing static but not dynamic facial expressions (Adolphs et al., 1994, 2003), and they are able to produce an imitation of a facial expression on demand (Anderson et al., 2000).

The present study focussed on neutral and emotionally expressive instrumental actions and aimed at clarifying the specific contribution of dynamic information to the perception of fearful body expression. Furthermore, our approach allows us to clarify the relation between processing the fear signal provided by whole body actions in emotional and motor areas. Using event-related fMRI and a factorial design, we compared neutral and fear expressing whole body actions and their scrambled counterparts presented in either still or dynamic images. Our goals were to identify the neural circuits that are specifically involved in the perception of an action involving the whole body condition specific effects of fear and the combined effect of fear and dynamic action information.

Materials and methods

Participants

Sixteen right-handed subjects (6 men and 10 women, mean age 25 years) with no neurological or psychiatric history participated in the imaging study. All gave informed consent according to institutional guidelines of the local ethics committee (CMO region Arnhem-Nijmegen, The Netherlands). The study was conducted in accordance with the principles and guidelines in the Declaration of Helsinki.

Stimuli and experimental design

Materials

Construction of materials started with the recording of video films. A group of twelve semi-professional actors (six male), all graduates from a professional acting school, were hired in order to account for variability in acting style. They were paid for their services. Under professional direction they enacted different scenarios corresponding to fearful and neutral situations. In the scenario used in the present experiment the actors were instructed to open the door in front of them, react to the encounter and close the door again. The fear script required the actors to open the door and face a threat. For the "neutral scenario", the actors were required to open the same door. Performance was repeated until deemed satisfactory by the director. Recordings were made with the camera positioned directly facing the door viewed from the outside.

Videos were computer edited and a continuous fragment of 3 s (25 frames per second) was selected from initial materials, which had an average length of 5 s. The faces were then blurred using the After-effect software, such that only information from the body was available.

Selection of the stimuli was based on the results of a pilot study ($n=12$) using the edited video clips. A total of 141 video clips were presented on a PC screen with a 2 s interval. Participants were instructed to categorise each stimulus in a forced-choice procedure by pressing one of the three response buttons (fear, anger and neutral scenarios). For fear videos recognition rate was between 70 and 88% (average 79%), and for neutral ones, it was between 93 and 100% (average 97%). Finally, the highest ranked videos (average fear 86%, average neutral 97%) were chosen for use in the present study (12 actors*2 fear scenarios+12 actors*2 neutral scenarios). Static materials were obtained by selecting the frame at the perceived apex of the expression. In addition, 24 scrambled video clips and 24 scrambled static images were derived from the 24 neutral video clips and the 24 static neutral images. To do so, we used After-effect software to apply mosaic effects on each video clip or image.

fMRI experimental design (Fig. 1)

During the scanning session, a total of 422 stimuli were presented corresponding to 24 stimuli for each category (dynamic fear, static fear, dynamic neutral, static neutral, scrambled dynamic neutral and scrambled static neutral body expressions), 15 oddball stimuli (upside-down video clips) and 52 null events (black screen) presented twice Fig. 1. These 211 stimuli were fully randomised. Subjects were asked to press the button each time an upside-down video clip appeared such that trials of interest were uncontaminated by motor response.

fMRI data acquisition

Gradient-echo T_2^* -weighted transverse echo-planar images (EPI) with blood oxygenation level-dependent (BOLD) contrast were acquired with a 1.5 T Siemens SONATA scanner (Siemens, Erlangen, Germany). Each volume comprised 43 axial slices (TR=3790 ms, TE=40 ms, 2.5 mm thickness with 0.5 mm gap, FP=90°, FOV=32 cm), acquired sequentially in an ascending direction. An automatic shimming procedure was performed before each scanning session. A total of 448 functional volumes were collected for each subject. At the end of the scanning session, high-

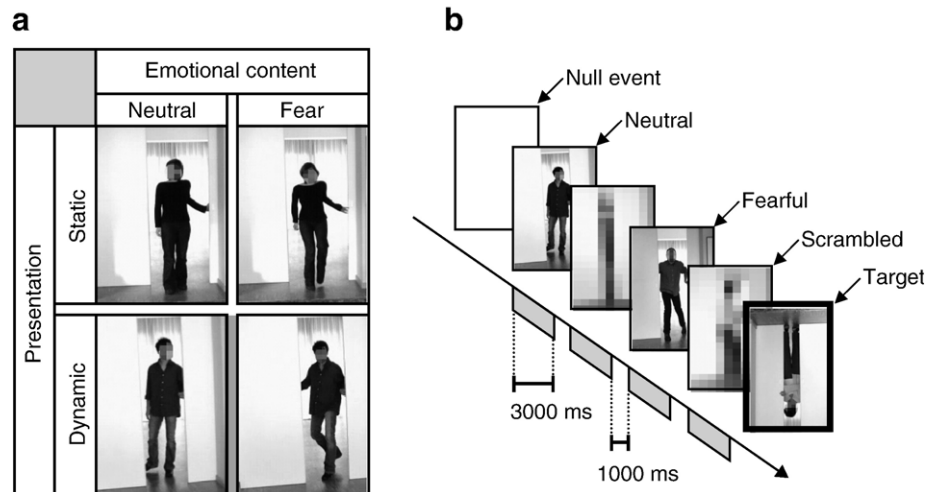


Fig. 1. Design and example of the stimuli. (a) 2*2 factorial design. Images were either static or dynamic and consisted of whole body images of actors opening a door in a neutral or fearful mode. (b) Example of a run and timing. Participants were instructed to press a button when they view an upside-down video clip interspersed among a run of body expressions (50% of the trials), scrambled (25%) and null stimuli (25%). Targets were odd trials (10%). Stimuli were presented for 3000 ms, with a 1000 ms gap in between during which a black screen was present.

resolution anatomical images were acquired using a TFL sequence (TE=3.68 ms, TR=2250 ms, voxel size=1*1*1 mm, 176 sagittal slices, FOV=256 mm).

Statistical Parametric Mapping

Image analysis was performed with SPM2 (Statistical Parametric Mapping, <http://www.fil.ion.ucl.ac.uk/spm>). The first five volumes of each functional run were discarded to allow for T1 equilibration effects. The remaining 443 functional images were reoriented, slice-time corrected to the middle slice and spatially realigned to the first volume. These images were normalised to the standard MNI template and subsampled at an isotropic voxel size of 2 mm. The normalised images were smoothed with an isotropic 6-mm full-width-half-maximum (FWHM) gaussian kernel.

Statistical analysis was carried out using Statistical Parametric Mapping (SPM2; Wellcome Department of Imaging Neuroscience, London, UK). A random effects analysis was performed. At the first level, the 9 following conditions were modelled for each subject: two trials where subjects perceived fear body expressions, presented in a static (Fs) or dynamic way (Fd), two trials where subjects perceived neutral body expressions presented in a static (Ns) or dynamic way (Nd). Finally, two represented the trials where subjects perceived scrambled stimuli presented in a static (Ss) or dynamic way (Sd), and one the oddball stimuli (Odd). The null events were modelled implicitly. The BOLD response to the stimulus onset for each event-type was convolved with the canonical haemodynamic response function of 3 s (0.79 TR). Also included for each subject's session were six covariates in order to capture residual movement-related artefacts (the 3 rigid-body translations and the 3 rotations determined from initial registration) and a single covariate representing the mean (constant) over scans. The data were high-pass filtered with a frequency cut-off at 128 s.

A within subjects ANOVAs was implemented in SPM2. To do this, we first created images of parameter estimates for 6 *t*-test contrasts of interest (Fs, Fd, Ns, Nd, Sd, Ss) for each subject at the

first-level analysis. These images were then entered into a second-level analysis using within subjects ANOVAs with 6 HRFs comprising a factor. A non-sphericity correction was applied for variance differences between conditions or subjects. The following contrasts were calculated at the random level:

1. Main effects of bodies vs. scrambled stimuli $(F_s + F_d + N_d + N_s) - 2(S_d + S_s)$.
2. Main effects of fear vs. neutral bodies $[(F_s + F_d) - (N_s + N_d)]$.
3. Main effects of dynamic vs. static bodies $[(F_d + N_d) - (F_s + N_s)]$.
4. Interaction between fear bodies and dynamic presentations $[(F_d - F_s) - (N_d - N_s)]$. The interaction was masked (inclusive) with the simple main effect of fear dynamic versus fear static $(F_d - F_s)$ at $p=0.001$ in order to reveal only activations that were specific to the perception of dynamic fear bodies.

The statistical parametric maps were thresholded at $p < 0.001$ (uncorrected for multiple comparisons), and activation foci with a minimum cluster size of 10 voxels are reported here. These maps were overlaid on the MNI single subject template and on the normalised structural images of each subject, and labelled using the atlas of [Duvernoy \(1999\)](#).

Results

fMRI results

The first analysis determined which activations were specific to the perception of bodies. The main effect of perceiving bodies as compared to scrambled stimuli was calculated: $[(F_d + F_s + N_d + N_s) - 2(S_d + S_s)]$, where Fs=static fear bodies; Fd=dynamic fear bodies; Ns=static neutral bodies; Nd=dynamic neutral bodies; Ss=static scrambled bodies; Sd=dynamic scrambled bodies. The analysis showed bilateral activations in the occipital and temporal poles, in the motion area MT/V5/EBA, in fusiform gyrus, in the hippocampus and in the right

amygdala. In addition, activations were revealed bilaterally in the lateral orbital gyrus, and in the medial orbital gyrus as well as in the medial part of the superior frontal gyrus. The full list of activations is given in Table 1. Examination of the parameter estimates in the amygdala indicates that the level of activity in that region is independent of whether the stimuli were static or dynamic (see Fig. 2c).

Data were then analysed according to the presence of emotion by calculating the main effect of perceiving fearful versus neutral bodies, irrespective of whether the stimuli were static or dynamic: $[(Fs+Fd)-(Ns+Nd)]$. This analysis yielded activations located bilaterally in the temporal pole and in the superior temporal sulcus. In addition, the medial superior frontal gyrus, the inferior frontal and posterior orbital gyrus and the supramarginal gyrus were activated in the right hemisphere. The full list of activations is given in Table 2. Examination of the parameter estimates in the temporal pole indicates that the level of activity in that region is sensitive to dynamic motion information as it appears to be higher during the fear dynamic condition compared to the static one ($xyz = -22\ 10\ -26$, $p < 0.001$) (see Fig. 3c).

Furthermore, we analysed the data according to whether the images were dynamic or static by calculating the main effect of perceiving dynamic versus static body expressions, irrespective of the emotional content $[(Fd+Nd)-(Fs+Ns)]$. The analysis showed bilateral activations in the fusiform gyrus, the middle occipital and temporal gyrus, the superior temporal sulcus, the temporo-parietal junction, the intraparietal sulcus, the superior parietal lobe and the precentral gyrus. In the right hemisphere, the pre-SMA/superior frontal gyrus, the right inferior frontal and orbital gyrus were detected. In the left hemisphere, the SMA and pulvinar were activated. The full list of activations is given in Table 3.

The next analysis determined which activations were specific to the perception of dynamic fear bodies. The interaction between emotional content and dynamic presentation of bodies was calculated: $[(Fd-Fs)-(Nd-Ns)]$. The interaction was

Table 1

Brain regions activated during the perception of body expressions versus scrambled stimuli, irrespective of static or dynamic information

Brain regions	MNI coordinates			Z score
	x	y	z	
R medial superior frontal gyrus	4	54	28	4.29
L medial orbital gyrus	-2	44	-14	4.31
R lateral orbital gyrus	36	32	-20	4.15
L lateral orbital gyrus	-46	34	-14	3.78
R superior temporal sulcus (STSp)	60	-46	16	5.98
L superior temporal sulcus (STSp)	-54	-50	16	4.05
R thalamus (pulvinar)	13	-30	0	4.23
R hippocampus	24	-24	-14	4.10
L hippocampus	-22	-4	-32	3.74
R medial temporal pole	54	14	-26	4.58
L medial temporal pole	-32	12	-30	4.26
R temporal pole	26	10	-28	4.78
R amygdala	28	0	-28	4.48
R fusiform gyrus	44	-52	-22	7.81
L fusiform gyrus	-40	-56	-18	4.03
R MT/V5/EBA complex	52	-72	6	7.22
L MT/V5/EBA complex	-44	-82	4	4.08

$[(Fs+Fd+Ns+Nd)-2(ScD+ScS)]$.

$p < 0.001$ non-corrected.

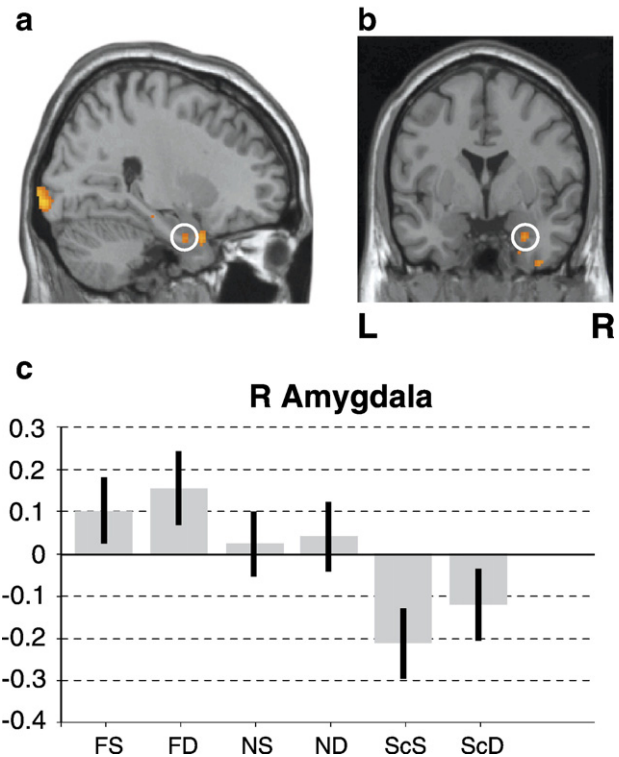


Fig. 2. All bodies vs. scrambled bodies. The right amygdala showing amplitude difference when subjects perceive bodies versus scrambled stimuli, irrespective of whether the stimuli are presented in a static or dynamic mode. (a) Group ($n=16$) average activation of the right amygdala superimposed on a sagittal section of the MNI brain. (b) Group ($n=16$) average activation of the right amygdala superimposed on a coronal section of the MNI brain. (c) Mean value of the parameter estimates (arbitrary units, mean centered) for the maxima of the right amygdala ($x, y, z = 28\ 0\ -28$) for fearful static body expressions (FS), fearful dynamic body expressions (FD), neutral static body expression (NS), neutral dynamic body expression (ND), scrambled static body expression (ScS) and scrambled dynamic body expression (ScD).

masked (inclusive) with the simple main effect of fear dynamic versus fear static ($Fd-Fs$) at $p=0.001$ in order to reveal only activations that were specific to the perception of dynamic fear bodies. This analysis showed activations bilaterally in superior temporal sulcus and in the temporo-parietal junction. In addition, the supramarginal gyrus at the level of the Jensen sulcus and the premotor cortex (PM) were detected in the right hemisphere (see Fig. 4). The full list of activations is given in Table 4.

Measure of the amount of movement

Finally, to test whether the differential activations between dynamic fearful and neutral expression are due to differences in movement characteristics we analysed the amount of movement per video clip and per condition by measuring the difference in movements between pairs of frames for each pixel. This difference was coded in terms of light intensity variation and averaged across pixels that scored higher than 10 (corresponding to the noise level of the camera). With this procedure, the mean movement score of each video clip was calculated and the

Table 2

Brain regions activated during the perception of fearful body expressions versus neutral whole body actions, irrespective of static or dynamic information

Brain regions	MNI coordinates			Z score
	x	y	z	
R pre-SMA/medial Superior frontal gyrus	8	18	66	4.03
L precuneus/transverse parietal sulcus	-12	-52	40	3.76
R temporo-parietal junction	64	-46	24	4.51
L superior temporal sulcus (pSTS)	-58	-54	14	4.36
R superior temporal sulcus (pSTS)	52	-48	12	4.11
R middle temporal gyrus (MT/V5/EBA)	48	-66	8	3.67
R inferior frontal gyrus (pars orbitalis)	50	30	-4	3.44
R superior temporal sulcus (middle part)	48	-20	-8	3.96
R posterior orbital gyrus	34	28	-16	4.06
R medial temporal lobe	34	4	-24	4.39
R temporal pole	44	18	-32	4.28
L temporal pole	-32	14	-32	3.81

[(Fd + Fs) - (Nd + Ns)].
 $p < 0.001$ non-corrected.

temporal profiles frame by frame for each condition were graphically represented. There was no difference in the mean scores reflecting the amount of movement between dynamic fearful body expression (mean score=40.25, SD=8.01) and

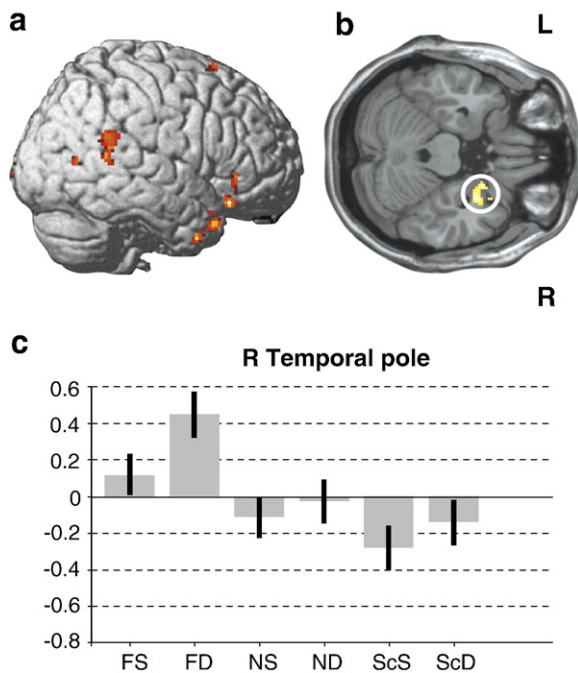


Fig. 3. Fear vs. neutral bodies. Regions showing amplitude difference when subjects perceive fearful versus neutral body expressions, irrespective of whether the stimuli are presented in a static or dynamic mode. (a) Group ($n=16$) average activations for the main effect of fear vs. neutral bodies, rendered on the MNI brain. Note the activations of the STS, the temporal pole and the inferior frontal gyrus. (b) Group ($n=16$) average activation of the right temporal pole superimposed on a horizontal section of the MNI brain. (c) Mean value of the parameter estimates (arbitrary units, mean centered) for the maxima of the right temporal pole ($x, y, z=24\ 12\ -24$), other conventions as in Fig. 2c.

Table 3

Brain regions activated during the perception of dynamic versus static body expression, irrespective of the emotional content

Brain regions	MNI coordinates			Z score
	x	y	z	
R SMA	10	0	70	3.89
L and R superior parietal lobe	±22	-62	62	4.55
R medial superior parietal lobe/precuneus	6	-56	66	4.47
L and R intraparietal sulcus	±34	-46	56	4.08
L and R dorsal precentral gyrus	±44	6	48	5.32
L and R intraparietal/postcentral sulcus	±30	-40	48	4.06
L and R posterior part of intraparietal sulcus	±24	-84	28	4.48
L and R temporo-parietal junction (STS-SMG)	±60	-42	30	5.42
R inferior frontal sulcus	50	28	24	4.01
R lateral orbital gyrus	50	30	-12	4.56
L pulvinar	-16	-24	10	3.66
L and R superior temporal sulcus (STS)	±60	-44	16	Inf/6.37
L and R middle temporal gyrus (MT/V5/EBA)	±48	-66	8	Inf
L and R middle occipital gyrus	±30	-94	8	5.43
R superior temporal sulcus (middle part)	54	-16	-14	4.77
L and R fusiform	±44	-50	-22	4.97
R medial temporal pole	24	10	-28	3.93
L cerebellum	-10	-76	-42	3.4

$p < 0.001$ non-corrected. SMG: supramarginal gyrus.
 [(Fd+Nd)-(Fs+Ns)].

dynamic neutral body expression (mean score=40.03, SD=4.82) [2 tailed t -test, $p=0.916$].

Discussion

The present study aimed at clarifying the relation between brain areas which play a critical role in processing EBL corresponding to an action, the supplementary fear signals provided by EBL and the relation between the activations corresponding to the viewing of dynamic fear actions. Our critical findings are threefold. Viewing the action by itself enhances amygdala activity; there is condition specific activation in the temporal pole and lateral orbital cortex elicited when the action expresses fear; and a significant interaction in STS and PM obtained when this fear expression action is shown in dynamic images.

First, the observed amygdala activation is consistent with the literature yet expands it significantly. In line with previous results in monkeys as well as in humans (Brothers, 1990; Brothers and Ring, 1993; Whalen et al., 2001; de Gelder et al., 2004), we show that seeing actions induces amygdala activation. The amygdala plays a crucial role in the neural circuitry by which the affective significance of information is encoded (Adolphs, 2002; Dolan, 2002) whether the stimuli are explicitly social (Aggleton and Passingham, 1981) or not (LeDoux, 2000). In macaque monkey, the visual input reaches the amygdala via a cortical route involving visual areas and the STS (Stefanacci and Amaral, 2000) as well as via a subcortical route involving the superior colliculus (LeDoux, 1996). The fact that the amygdala is activated in all conditions where a whole bodily action is contrasted to its scrambled counterpart may in part be related to the instrumental action used here. In contrast to grasping a glass on the table (Grosbras and Paus, 2006), the action used in the present study may invite by itself already a social meaning.

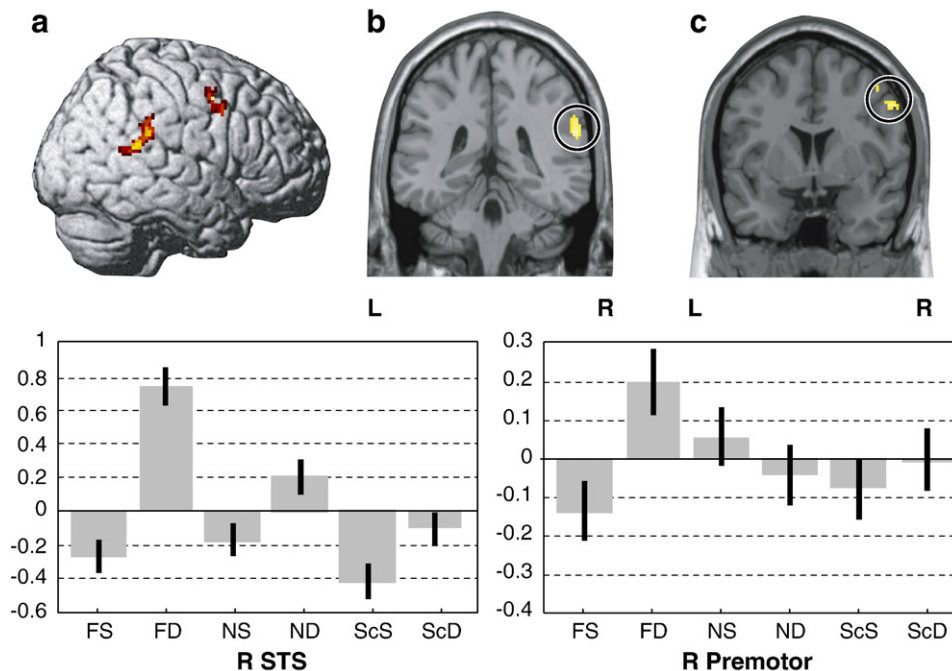


Fig. 4. Dynamic fear bodies. Regions detected in the interaction between fearful and dynamic body expressions, showing amplitude difference only when subjects perceive fearful dynamic body expressions. (a) Group ($n=16$) average activations of the right superior temporal sulcus (STS) and right premotor cortex (PM) rendered on the MNI brain. (b) Group ($n=16$) average activation of the right temporo-parietal junction superimposed on a coronal section of the MNI brain. (c) Group ($n=16$) average activation of the right premotor cortex superimposed on a coronal section of the MNI brain. (d) Mean value of the parameter estimates (arbitrary units, mean centered) for the maxima of the right temporo-parietal junction ($x, y, z=60 -42 18$), other conventions as in Fig. 3c. (e) Mean value of the parameter estimates (arbitrary units, mean centered) for the maxima of the right premotor cortex ($x, y, z=54 5 40$), other conventions as in Fig. 2c.

Interestingly, and consistent with this, it appears from post hoc exploration (Fig. 2) that the amygdala is not sensitive to dynamic motion information as its level of activity appears to be the same during the neutral dynamic condition compared to the static one. At first sight this result is surprising in view of electrophysiological studies in monkeys (Brothers et al., 1990; Brothers and Ring, 1993; Nishijo et al., 2003) and neuroimaging studies in humans (Bonda et al., 1996; Kawashima et al., 1999; LaBar et al., 2003; Sato et al., 2004) showing that amygdala is sensitive to biological movements, even when the observed situation is not specifically emotional (Brothers, 1990; Brothers and Ring, 1993; Nishijo et al., 2003). However, for the purpose of a narrowly focused comparison we used the same instrumental actions in all conditions rather than relying on the comparison between a neutral instrumental action (combing hair) vs. a bodily expression of

emotion (as in de Gelder et al., 2004). The resulting amygdala activation is not significantly modulated by adding either fear or dynamic information.

In addition to the amygdala, we observed right hemispheric activations in the temporal pole (TP) and lateral orbital cortex (VLPFC, BA 47) specifically for fear expressing actions. These two brain areas have an important role in emotion (for recent reviews, see Bechara et al., 2000; Elliott et al., 2000; Kringelbach and Rolls, 2004). From monkey data, it is known that the temporopolar cortex is the site of convergence of sensory and limbic inputs (Moran et al., 1987). Furthermore, the amygdala's major projection to temporal cortex is the temporal pole, whereas its heaviest projections to prefrontal cortex terminate in medial and lateral orbital cortex, including the lateral area 12 in monkey, which corresponds to the pars orbitalis of the inferior frontal gyrus in human (BA 47) (Amaral and Price, 1984). Finally, the lateral orbitofrontal cortex also receives direct visual information both from the temporal pole and superior temporal sulcus (Barbas, 1988). This triadic network linking amygdala, orbitofrontal and anterior TP is suggested to play a crucial role in processing emotional significance of events (Ghashghaei and Barbas, 2002). For example, Anderson et al. (2000) and Adolphs et al. (2001) observed higher deficits in recognition of facial emotions after right than left temporal pole lesions. Interestingly, the deficits observed after right temporal pole lesions mainly concern the processing of emotions that are associated with withdrawal or avoidance, such as fear (Adolphs et al., 2001; Anderson et al., 2000). Similarly, fronto-temporal dementia affecting the orbitofrontal cortex is associated with a gradual tendency to withdraw from social interactions (Rahman et al., 1999). Besides its direct

Table 4

Brain regions activated for the interaction between fearful body expression and dynamic information

Brain regions	MNI coordinates			Z score
	x	y	z	
R premotor cortex	54	4	40	4.08
R temporo-parietal junction (STS-SMG)	60	-36	24	4.46
L temporo-parietal junction (STS-SMG)	-52	-42	24	3.75
L superior temporal sulcus (STS)	-52	-54	20	3.76
R supramarginal gyrus (Jensen sulcus)	60	-44	18	4.42
R superior temporal sulcus (STS)	50	-44	22	3.32

[(Fd - Fs) - (Nd - Ns)], masked (inclusive) by (Fd - Fs), $p=0.001$. $p < 0.001$ non-corrected. SMG: supramarginal gyrus.

role in processing emotions, temporal pole activation is often found in neuroimaging studies investigating the ability to mentalise or to attribute mental states to others (Baron-Cohen et al., 2000; Brunet et al., 2000; Castelli et al., 2000; Gallagher et al., 2000; Berthoz et al., 2002). The present enhanced activation in TP during perception of fearful actions is coherent with its suggested role in generating a wider emotional context for the stimuli being processed and in retrieving personal experience from memory (Gallagher and Frith, 2003; Frith and Frith, 2003). Previous studies have also reported activation in VLPFC during passive viewing of emotional stimuli (Blair et al., 1999) and of expressive gesture (Gallagher and Frith, 2004; Lotze et al., 2006). Moreover, the more intense an emotion was perceived, the more activity was detected in the VLPFC (Grimm et al., 2006).

The interaction between fearful vs. neutral and dynamic vs. static actions did reveal STS-temporo-parietal junction and premotor cortex (PM) activations. These two areas are well known for their role in processing biological movement and action representation. In the macaque temporal cortex, neurons within the STS react to complex social signals like facial expressions and body images (Perrett et al., 1989). Similarly, in humans, STS selectively responds to the perception of biological motion, such as hand, mouth and eye movements (for a review, see Allison et al., 2000). In the PM area F5 of the macaque monkey “mirror” neurons discharge not only when the monkey observes the experimenter or another monkey performing an action but also when the monkey performs the same action (di Pellegrino et al., 1992; Fogassi et al., 1998). In humans, the STS, the parietal and the PM cortex are activated during action observation (Grafton et al., 1996; Rizzolatti et al., 1996; Grèzes et al., 2003; Buccino et al., 2001). The automatic activation of action representations during action observation was suggested to be at the basis of action understanding (Grèzes and Decety, 2001; Gallese et al., 2004; Iacoboni, 2005; Sommerville and Decety, 2006) and was also recently put forward as an essential component of understanding emotions (Preston and de Waal, 2002; Carr et al., 2003; Gallese et al., 2004). The present activations in the STS and PM cortex do not simply reflect a quantitative difference in low-level motion information between fearful and neutral videos as both conditions score similarly when we quantify the movement component. Yet, one possible explanation of enhanced activation in STS and PM cortex specifically for dynamic expression of emotion is that, when viewing dynamic fear bodies, an important priority for the brain is to represent the perceived emotional action. This is in line with Adolphs et al. (2003)’s findings that patient B with extensive lesion of the ventral pathway, which includes the amygdala, is able to recognise emotions from dynamic facial expression but not from static one.

However, besides their communicative function, emotions are also adaptive in the sense that they prepare the organism for behavioural response to the current environment (Darwin, 1872; Frijda, 1986; Lazarus, 1991; LeDoux, 1996). A substantial number of studies have indeed shown that lesions of the amygdala not only disrupt the ability to process fear signals (LeDoux, 2000) but also can abolish characteristic fear behaviour in primates (Bauman et al., 2004; Emery et al., 2004). In this model, the amygdala plays a critical role in initiating adaptive behavioural response to the perception of social signals, via its connections with subcortical areas, such as the hypothalamus, striatum and basal cortex, or via the PM cortex (Amaral and Price, 1984; Avendano et al., 1983). The present PM activation ($z=40$), revealed by the interaction, is located

behind the ventral limb of the precentral sulcus and thus lies at the border between the ventral (PMv) and dorsal (PMd) part of the PM cortex. The ventral section of PMd receives direct input from STS (Luppino et al., 2001). The dorsal PM cortex is implicated in motor preparation and environmentally triggered actions (Hoshi and Tanji, 2004; Passingham, 1993). Interestingly, electrical stimulation of the dorsal polysensory area of PMv evokes a specific set of defensive (avoiding, protecting, withdrawing) movements (Cooke and Graziano, 2004; Graziano et al., 2002). In the present study, the actors express fear by withdrawing from the door. Thus it is not possible to disentangle whether the activations detected in PM cortex during the perception of emotions predominantly reveal motor simulation in the observer of the action perceived or alternatively the preparation of the observers’ motor response required by the situation. This important issue must be addressed in future research.

Acknowledgments

We are grateful to I. Toni for discussions on methods, to P. Gaalman for his technical assistance and to W. van de Riet for assistance with recruiting participants. We thank R.E. Passingham for advice and comments on the paper. JG, SP and BdG were partly supported by Human Frontier Science Program HFSP-RGP0054/2004-C and FP6-2005-NEST-Path Imp 043403.

References

- Adolphs, R., 2002. Neural systems for recognizing emotion. *Curr. Opin. Neurobiol.* 12, 169–177.
- Adolphs, R., Tranel, D., Damasio, H., Damasio, A., 1994. Impaired recognition of emotion in facial expression following bilateral damage to the human amygdala. *Nature* 372, 653–658.
- Adolphs, R., Tranel, D., Damasio, H., 2001. Emotion recognition from faces and prosody following temporal lobectomy. *Neuropsychology* 15 (3), 396–404.
- Adolphs, R., Tranel, D., Damasio, A.R., 2003. Dissociable neural systems for recognizing emotions. *Brain Cogn.* 52, 61–69.
- Aggleton, J.P., Passingham, R.E., 1981. Syndrome produced by lesions of the amygdala in monkeys (*Macaca mulatta*). *J. Comp. Physiol. Psychol.* 95, 961–977.
- Allison, T., Puce, A., McCarthy, G., 2000. Social perception from visual cues: role of the STS region. *Trends Cogn. Sci.* 4, 267–278.
- Amaral, D.G., Price, J.L., 1984. Amygdalo-cortical projections in the monkey (*Macaca fascicularis*). *J. Comp. Neurol.* 230, 465–496.
- Anderson, A.K., Spencer, D.D., Fulbright, R.K., Phelps, E.A., 2000. Contribution of the anteromedial temporal lobes to the evaluation of facial emotion. *Neuropsychology* 14 (4), 526–536.
- Atkinson, A.P., Dittrich, W.H., Gemmell, A.J., Young, A.W., 2004. Emotion perception from dynamic and static body expressions in point-light and full-light displays. *Perception* 33 (6), 717–746.
- Avendano, C., Price, J.L., Amaral, D.G., 1983. Evidence for an amygdaloid projection to premotor cortex but not to motor cortex in the monkey. *Brain Res.* 264, 111–117.
- Barbas, H., 1988. Anatomic organization of basoventral and mediadorsal visual recipient prefrontal regions in the rhesus monkey. *J. Comp. Neurol.* 276 (3), 313–342.
- Baron-Cohen, S., Ring, H.A., Bullmore, E.T., Wheelwright, S., Ashwin, C., Williams, S.C., 2000. The amygdala theory of autism. *Neurosci. Biobehav. Rev.* 24 (3), 355–364.
- Bauman, M.D., Lavenex, P., Mason, W.A., Capitanio, J.P., Amaral, D.G., 2004. The development of social behavior following neonatal amygdala lesions in rhesus monkeys. *J. Cogn. Neurosci.* 16, 1388–1411.

- Bechara, A., Tranel, D., Damasio, H., 2000. Characterization of the decision-making deficit of patients with ventromedial prefrontal cortex lesions. *Brain* 123 (Pt 11), 2189–2202.
- Berthoz, S., Armony, J.L., Blair, R.J.R., Dolan, R.J., 2002. An fMRI study of intentional and unintentional (embarrassing) violations of social norms. *Brain* 125, 1696–1708.
- Blair, R.J., Morris, J.S., Frith, C.D., Perrett, D.I., Dolan, R.J., 1999. Dissociable neural responses to facial expressions of sadness and anger. *Brain* 122 (Pt 5), 883–893.
- Bonda, E., Petrides, M., Ostry, D., Evans, A., 1996. Specific involvement of human parietal systems and the amygdala in the perception of biological motion. *J. Neurosci.* 16, 3737–3744.
- Brothers, L., 1990. The social brain: a project for integrating primate behavior and neurophysiology in a new domain. *Concepts Neurosci.* 1, 27–51.
- Brothers, L., Ring, B., 1993. Mesial temporal neurons in the macaque monkey with responses selective for aspects of social stimuli. *Behav. Brain Res.* 57, 53–61.
- Brothers, L., Ring, B., Kling, A., 1990. Response of neurons in the macaque amygdala to complex social stimuli. *Behav. Brain Res.* 41, 199–213.
- Brunet, E., Sarfati, Y., Hardy-Bayle, M.C., Decety, J., 2000. A PET investigation of the attribution of intentions with a nonverbal task. *NeuroImage* 11, 157–166.
- Buccino, G., Binkofski, F., Fink, G.R., Fadiga, L., Fogassi, L., et al., 2001. Action observation activates premotor and parietal areas in a somatotopic manner: an fMRI study. *Eur. J. Neurosci.* 13, 400–404.
- Carr, L., Iacoboni, M., Dubeau, M.C., Mazziotta, J.C., Lenzi, G.L., 2003. Neural mechanisms of empathy in humans: a relay from neural systems for imitation to limbic areas. *Proc. Natl. Acad. Sci. U. S. A.* 100, 5497–5502.
- Castelli, F., Happé, F., Frith, U., Frith, C.D., 2000. Movement and mind: a functional imaging study of perception and interpretation of complex intentional movement patterns. *NeuroImage* 12, 314–325.
- Cooke, D.F., Graziano, M.S.A., 2004. Sensorimotor integration in the precentral gyrus: polysensory neurons and defensive movements. *J. Neurophysiol.* 91, 1648–1660.
- Darwin, C., 1872. *The Expression of the Emotions in Man and Animals*. John Murray, London.
- Decety, J., Chaminade, T., 2003. When the self represents the other: a new cognitive neuroscience view on psychological identification. *Conscious. Cogn.* 12, 577–596.
- de Gelder, B., Snyder, J., Greve, D., Gerard, G., Hadjikhani, N., 2004. Fear fosters flight: a mechanism for fear contagion when perceiving emotion expressed by a whole body. *Proc. Natl. Acad. Sci.* 101, 16701–16706.
- di Pellegrino, G., Fadiga, L., Fogassi, L., Gallese, V., Rizzolatti, G., 1992. Understanding motor events: a neurophysiological study. *Exp. Brain Res.* 91, 176–180.
- Dittrich, W.H., Troscianko, T., Lea, S.E., Morgan, D., 1996. Perception of emotion from dynamic point-light displays represented in dance. *Perception* 25 (6), 727–738.
- Dolan, R.J., 2002. Emotion, cognition, and behavior. *Science* 298, 1191–1194.
- Duvernoy, H., 1999. *The Human Brain. Surface, Blood Supply and Three-dimensional Sectional Anatomy*. Springer Verlag, New-York.
- Elliott, R., Dolan, R.J., Frith, C.D., 2000. Dissociable functions in the medial and lateral orbitofrontal cortex: evidence from human neuroimaging studies. *Cereb. Cortex* 10 (3), 308–317 (Review).
- Emery, N.J., Capitanio, J.P., Mason, W.A., Machado, C.J., Mendoza, S.P., Amaral, D.G., 2004. The effects of bilateral lesions of the amygdala on dyadic social interactions in rhesus monkeys (*Macaca mulatta*). *Behav. Neurosci.* 115, 515–544.
- Fogassi, L., Gallese, V., Fadiga, L., Rizzolatti, G., 1998. Neurones responding to the sight of goal-directed hand/arm actions in the parietal area PF7b of the macaque monkey. *Abst.-Soc. Neurosci.* 24, 257.5.
- Frijda, N.H., 1986. *The Emotions*. Cambridge Univ. Press, Cambridge.
- Frith, U., Frith, C.D., 2003. Development and neurophysiology of mentalizing. *Philos. Trans. R. Soc. Lond., B Biol. Sci.* 358 (1431), 459–473.
- Gallagher, H.L., Frith, C.D., 2003. Functional imaging of ‘theory of mind’. *Trends Cogn. Sci.* 7 (2), 77–83.
- Gallagher, H.L., Frith, C.D., 2004. Dissociable neural pathways for the perception and recognition of expressive and instrumental gestures. *Neuropsychologia* 42 (13), 1725–1736.
- Gallagher, H.L., Happé, F., Brunswick, N., Fletcher, P.C., Frith, U., Frith, C.D., 2000. Reading the mind in cartoons and stories: an fMRI study of « theory of mind » in verbal and non-verbal tasks. *Neuropsychologia* 38, 11–21.
- Gallese, V., Keysers, C., Rizzolatti, G., 2004. A unifying view of the basis of social cognition. *TICS* 8, 396–403.
- Ghashghaei, H.T., Barbas, H., 2002. Pathways for emotion: interactions of prefrontal and anterior temporal pathways in the amygdala of the rhesus monkey. *Neuroscience* 115 (4), 1261–1279.
- Graziano, M.S.A., Taylor, C.S.R., Moore, T., 2002. Complex movements evoked by microstimulation of precentral cortex. *Neuron* 34, 841–851.
- Grafton, S.T., Arbib, M.A., Fadiga, L., Rizzolatti, G., 1996. Localization of grasp representations in humans by positron emission tomography. 2. Observation compared with imagination. *Exp. Brain Res.* 112, 103–111.
- Grèzes, J., Decety, J., 2001. Functional anatomy of execution, mental simulation, observation, and verb generation of actions: a meta-analysis. *Hum. Brain Mapp.* 12, 1–19.
- Grèzes, J., Armony, J.L., Rowe, J., Passingham, R.E., 2003. Activations related to “Mirror” and “Canonical” neurones in the human brain: a fMRI study. *NeuroImage* 18, 928–937.
- Grimm, S., Schmidt, C.F., Bermpohl, F., Heinzel, A., Dahlem, Y., Wyss, M., Hell, D., Boesiger, P., Boeker, H., Northoff, G., 2006. Segregated neural representation of distinct emotion dimensions in the prefrontal cortex—An fMRI study. *NeuroImage* 30 (1), 325–340.
- Grosbras, M.H., Paus, T., 2006. Brain networks involved in viewing angry hands or faces. *Cereb. Cortex* 16, 1087–1096.
- Hadjikhani, N., de Gelder, B., 2003. Seeing fearful body expressions activates the fusiform cortex and amygdala. *Curr. Biol.* 13 (24), 2201–2205.
- Haxby, J.V., Hoffman, E.A., Gobbini, M.I., 2002. Human neural systems for face recognition and social communication. *Biol. Psychiatry* 51 (1), 59–67.
- Hoshi, E., Tanji, J., 2004. Functional specialization in dorsal and ventral premotor areas. *Prog. Brain Res.* 143, 507–511.
- Iacoboni, M., 2005. Neural mechanisms of imitation. *Curr. Opin. Neurobiol.* 15, 632–637 (Review).
- Kawashima, R., Sugiura, M., Kato, T., Nakamura, A., Hatano, K., Ito, K., Fukuda, H., Kojima, S., Nakamura, K., 1999. The human amygdala plays an important role in gaze monitoring. A PET study. *Brain* 1999 (122), 779–783.
- Kringelbach, M.L., Rolls, E.T., 2004. The functional neuroanatomy of the human orbitofrontal cortex: evidence from neuroimaging and neuropsychology. *Prog. Neurobiol.* 72 (5), 341–372 (Review).
- Jeannerod, M., 2001. Neural simulation of action: a unifying mechanism for motor cognition. *NeuroImage* 14, S103–S109.
- LaBar, K.S., Crupain, M.J., Voyvodic, J.T., McCarthy, G., 2003. Dynamic perception of facial affect and identity in the human brain. *Cereb. Cortex* 13, 1023–1033.
- Lazarus, R.S., 1991. *Emotion and Adaptation*. Oxford Univ. Press, London.
- LeDoux, J.E., 1996. *The Emotional Brain*. Simon and Schuster, New-York.
- LeDoux, J.E., 2000. Emotion circuits in the brain. *Annu. Rev. Neurosci.* 23, 155–184.
- Lotze, M., Heymans, U., Birbaumer, N., Veit, R., Erb, M., Flor, H., Halsband, U., 2006. Differential cerebral activation during observation of expressive gestures and motor acts. *Neuropsychologia* 44 (10), 1787–1795.
- Luppino, G., Calzavara, R., Rozzi, S., Matelli, M., 2001. Projections from the superior temporal sulcus to the agranular frontal cortex in the macaque. *Eur. J. Neurosci.* 14, 1035–1040.
- Moran, M.A., Mufson, E.J., Mesulam, M.M., 1987. Neural inputs into the temporopolar cortex of the rhesus monkey. *J. Comp. Neurol.* 256 (1), 88–103.

- Nishijo, H., Hori, E., Tazumi, T., Eifuku, S., Umeno, K., Tabuchi, E., Ono, T., 2003. Role of the monkey amygdala in social cognition. *Int. Congr. Ser.* 1250, 295–310.
- Passingham, R.E., 1993. *The Frontal Lobes and Voluntary Action*. Oxford Univ. Press, Oxford.
- Perrett, D.I., Harries, M.H., Bevan, R., Thomas, S., Benson, P.J., 1989. Frameworks of analysis for the neural representation of animate objects and actions. *J. Exp. Biol.* 146, 87–113.
- Preston, S.D., de Waal, F.B., 2002. Empathy: its ultimate and proximate bases. *Behav. Brain Sci.* 25 (1), 1–20 (discussion 20–71).
- Rahman, S., Sahakian, B.J., Hodges, J.R., Rogers, R.D., Robbins, T.W., 1999. Specific cognitive deficits in mild frontal variant frontotemporal dementia. *Brain* 122, 1469–1493.
- Rizzolatti, G., Fogassi, L., Gallese, V., 2001. Neurophysiological mechanisms underlying the understanding and imitation of action. *Nat. Rev., Neurosci.* 2, 661–670.
- Rizzolatti, G., Fadiga, L., Gallese, V., Fogassi, L., 1996. Localization of grasp representations in humans by PET: 1. Observation versus execution. *Exp. Brain Res.* 3, 131–141.
- Sato, W., Kochiyama, T., Yoshikawa, S., Naito, E., Matsumura, M., 2004. Enhanced neural activity in response to dynamic facial expressions of emotion: an fMRI study. *Brain Res. Cogn. Brain Res.* 20, 81–91.
- Sommerville, J.A., Decety, J., 2006. Weaving the fabric of social interaction: articulating developmental psychology and cognitive neuroscience in the domain of motor cognition. *Psychon. Bull. Rev.* 13, 179–200.
- Sprengelmeyer, R., Young, A.W., Schroeder, U., Grossenbacher, P.G., Federlein, J., Buttner, T., Przuntek, H., 1999. Knowing no fear. *Proc. Biol. Sci.* 266 (1437), 2451–2456.
- Stefanacci, L., Amaral, D.G., 2000. Topographic organization of cortical inputs to the lateral nucleus of the macaque monkey amygdala: a retrograde tracing study. *J. Comp. Neurol.* 421, 52–79.
- Wallbott, H.G., Scherer, K.R., 1986. Cues and channels in emotion recognition. *J. Pers. Soc. Psychol.* 51 (4), 690–699.
- Whalen, P.J., Shin, L.M., McInerney, S.C., Fischer, H., Wright, C.I., Rauch, S.L., 2001. A functional MRI study of human amygdala responses to facial expressions of fear versus anger. *Emotion* 1 (1), 70–83.