

Emotional modulation of visual and motor areas by dynamic body expressions of anger

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The ability to detect emotional meaning in others' behavior constitutes a central component of social competence. Expressions of anger in particular present salient signals that play a major role in the regulation of social interactions. Investigations of human anger signals have to date used still pictures of facial expressions but so far the neurobiological basis of bodily communication of anger remains largely unknown. Using functional magnetic resonance imaging, the present study investigated the neural bases involved in perceiving anger signals emanating from the whole body. Our study also investigates what the presence of dynamic information adds to the perception of body expressions of anger. Participants were scanned while viewing stimuli (stills or videos) of angry and neutral whole-body expressions. Whole-body expressions of anger elicit activity in regions including the amygdala and the lateral orbitofrontal cortex, which play a role in the affective evaluation of the stimuli. Importantly, the perception of dynamic body expressions of anger additionally engages the hypothalamus, the ventromedial prefrontal cortex, the temporal pole and the premotor cortex, brain regions that are coupled with autonomic reactions and motor responses related to defensive behaviors.

INTRODUCTION

The ability to detect nonverbal signals in others' actions and emotional expressions constitutes a central component of social competence. Expressions of anger in particular present salient signals that play a major role in the regulation of social interactions. Angry expressions signal a potential physical and/or symbolic attack (Schupp et al.,

2004), are perceived as threatening (Dimberg, 1986; Strauss et al., 2005) and trigger adaptive action in the observers (Frijda, 1986). To date, the neural basis of anger perception has been investigated mainly by presenting pictures of angry facial expressions (see Hennenlotter & Schroeder, 2006, for a review; also overview in Table 1). The lateral orbitofrontal cortex (OFC), amygdala, superior frontal gyrus, premotor cortex

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TABLE 1

Overview of brain regions detected in previous neuroimaging studies during the presentation of facial expressions of anger

References	Modality	Brain regions								
		Lat OFC	AMG	mSFG	PM	FF	ACC	PCC	TP	IFG
Blair, Morris, Frith, Perrett, & Dolan (1999) ^b	Still	X					X			
Esslen, Pascual-Marqui, Hell, Kochi, & Lehmann (2004) ^c	Still	X		X						
Fitzgerald, Angstadt, Jelsone, Nathan, & Phan (2006) ^{a*}	Still	X	X	X						
Grosbras & Paus (2006) ^{a*}	Dynamic		X		X	X				
Kesler-West et al. (2001) ^a	Still	X		X	X	X				
Kilts et al. (2003) ^b	Dynamic			X						X
Sprengelmeyer, Rausch, Eysel, & Przuntek (1998) ^a	Still	X						X		
Whalen et al. (2001) ^a	Still		X		X					
Williams et al. (2004) ^a	Still		X			X	X		X	

Notes: Inclusion criteria were an explicit (vs. subliminal) presentation of facial expressions of anger without aversive conditioning, and the presentation of results contrasting anger versus neutral (or baseline*) conditions. Note that the hypothalamus and the ventromedial prefrontal cortex were not detected in previous studies. Superscripts indicate the imaging method used (^afMRI, ^bPET and ^cEEG, respectively). Lat OFC: lateral orbitofrontal cortex (BA 47); AMG: amygdala; mSFG: medial superior frontal gyrus (BA 8, BA 9); PM: premotor cortex; FF: fusiform gyrus; ACC/PCC: anterior/posterior cingulate cortex; TP: temporal pole; IFG: inferior frontal gyrus (BA 45—pars triangularis).

and fusiform gyrus are often involved but there is considerable variability among the results obtained by different investigators, with the exception of lateral OFC, which is consistently identified across almost all studies (Murphy, Nimmo-Smith, & Lawrence, 2003).

Facial expressions of anger are an integral part of angry behavior that involves the whole body (de Gelder, 2006). Bodily expressions of anger are of prime importance in regulating social interactions and in negotiating aggressive confrontations in primates (Emery & Amaral, 2000) and in humans (Argyle, 1988). Once the scope of anger investigations is extended beyond individual facial expressions to whole-body behaviors, attention is drawn to two novel dimensions of anger signals. One is that whole-body expressions of emotion often do not simply consist of purely emotional expressions but show a person in the course of performing an action with an emotional overtone. Bodily expressions of emotion not only inform the observer about the state of mind but also show the actions being undertaken by the angry person, which may consist of a direct threat towards the observer. For example, a simple action of throwing a ball, when done in anger, may be perceived as an attack. Also, the more anger colors the action the more it may be perceived as a threat and elicit a defensive reaction in the observer. Neurophysiological findings indicate that when an animal is confronted with signals of danger, characteristic defensive responses like fight, flight or freezing

are elicited allowing the animal to shield from the source of threat (Blanchard & Blanchard, 1988; McNaughton & Corr, 2004). The amygdala is hypothesized to play a critical role in a network of brain structures mediating fear responses and triggering threat-related behaviors (Amaral, 2003; Blanchard & Blanchard, 1972; LeDoux, 2000) via its connections with other structures such as the medial prefrontal cortex and the hypothalamus (Ongur & Price, 2000).

Another dimension that comes to the foreground when we broaden the scope of emotion research and include the whole body concerns the contribution to emotion and action understanding from movement. So far the importance of movement has only been recently investigated for facial expressions of emotions using neuroimaging (Decety & Chaminade, 2003; Kilts, Egan, Gideon, Ely, & Hoffman, 2003; LaBar, Crupain, Voyvodic, & McCarthy, 2003; Sato, Kochiyama, Yoshikawa, Naito, & Matsumura, 2004; Simon, Craig, Miltner, & Rainville, 2006). Better recognition rates for movies than for still images have also been reported for body stimuli (Atkinson, Dittrich, Gemmell, & Young, 2004; de Meijer, 1989). To our knowledge only three functional brain imaging studies have explored the perception of dynamic expressions of anger using either facial expressions (Kilts et al., 2003; LaBar et al., 2003) or hand actions (Grosbras & Paus, 2006).

Here our goal was to investigate the brain regions involved in perceiving anger signals emanating from the whole body. Using event-related fMRI, we scanned participants while they viewed

short movies and still images of neutral and angry whole-body actions. We predicted: (1) that whole-body actions expressing anger would be perceived as threat signals and would consequently enhance the level of activation in amygdala and in high-level visual cortices; (2) furthermore, that they would elicit activity in frontal regions, particularly in the lateral OFC (see Table 1); and, finally, (3) that there would be a significant interaction between emotional and motor processes during the perception of dynamic whole-body expressions of anger.

METHODS

Participants

Sixteen right-handed subjects (7 females and 9 males, ranging from 18 to 26 years of age) with no neurological or psychiatric history participated in the imaging study. All provided written informed consent according to institutional guidelines of the local ethics committee (CMO region Arnhem–Nijmegen, The Netherlands).

Materials

Construction of materials started with the recording of video films. In order to account for variability in acting style, a large group of actors was hired (6 males and 6 females). All actors were graduates from professional acting schools and they performed different scenarios familiar from daily life under professional direction. For the scenario used in the present experiment the actors were instructed to open the door in front of them, react to a specified encounter and close the door again. The anger version of this scenario required the actors to open the door and react to something or someone that made them angry. The performance was repeated till deemed satisfactory by the director. Recordings were made with a video camera positioned directly in front of the door viewed from the outside. The video films were then 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. Subsequently the faces were blurred using the After-effect software (Adobe®), such that only information from the body was available.

From these edited materials a subset was used for stimuli in the present experiment. 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 (fear, anger and neutral door-opening scenarios) were presented individually to participants on a PC screen with a 2 s interval. Participants were instructed to categorize each stimulus in a forced-choice procedure by pressing one of the three response buttons corresponding to each type of scenario. Average recognition rate for anger and neutral scenarios was 76% ($SD = 28$) and 97% ($SD = 5$), respectively. The 48 highest-ranked videos, average recognition of anger 89% ($SD = 15$) and of neutral 97% ($SD = 5$), were chosen for use in the present study (12 actors \times 2 anger scenarios + 12 actors \times 2 neutral scenarios). To check whether there were quantitative differences in movement between anger and neutral movies, we estimated the amount of movement per video clip by quantifying the variation of light intensity (luminance) between pairs of frames for each pixel. For each frame ($n = 75 - 1$), these differences were averaged across pixels that scored (on a scale reaching a maximum of 255) higher than 10, a value which corresponds to the noise level of the camera. These estimations were then averaged for each movie and the resulting scores were used to test the hypothesis of a difference in movement between neutral and anger movies. No significant difference was detected (Student's two-tailed t -test, $p = .64$).

A total of 116 still images was obtained from the selected anger, fear and neutral video clips by sampling in each video one or two frames judged to be at the apex of the expression. Selection of the stimuli was then based on the results of a pilot study ($n = 14$). Participants were shown the 116 images of bodies expressing fear or anger as well as the neutral actions. Each picture was presented for 3 s on a PC screen with a 3 s interval. Participants were instructed to categorize each stimulus in a forced-choice procedure by pressing one of the three response buttons corresponding to the three situations. The 24 highest-ranked anger pictures (average recognition rate 68%, $SD = 30$) and the 24 highest-ranked neutral pictures (average recognition rate 78%, $SD = 16$) were selected for use in the present study.

Finally, 24 scrambled video clips and 24 scrambled static images were derived from the videos and still images to serve as control conditions. This was done with After-effect software

(Adobe®) and consisted in applying a mosaic effect on each video clip and image. This creates a low-resolution effect by filling a layer with solid rectangles colored with the average color of the corresponding region in the unaffected layer.

Experimental design

During the scanning session, a total of 462 stimuli were presented, consisting of 24 stimuli for each of the 6 conditions: anger dynamic (Ad), anger static (As), neutral dynamic (Nd), neutral static (Ns), scrambled neutral dynamic (Sd) and scrambled neutral static (Ss), as well as 15 oddball stimuli (upside-down neutral video clips) and 72 null events (black screens). The stimuli were presented twice and the experiment was split in two contiguous sessions with the event order fully randomized between subjects. Each stimulus lasted 3 s followed by a 960 ms black interval. Visual stimuli were back projected on a screen located behind the subject's head and were viewed inside the head coil using a mirror. The vertical and horizontal size of the stimuli was about 18 and 12 degrees. Participants were asked to press a button each time an oddball stimulus

appeared such that trials of interest were uncontaminated by motor response (Figure 1). Following the scanning session, subjects were asked to explicitly categorize the stimuli as neutral or angry body expressions (see behavioral results).

Data analysis

Gradient-echo T2*-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 contained 43 axial slices, repetition time (TR) = 3790 ms, echo time (TE) = 40 ms, 2.5 mm thickness with 0.5 mm gap, flip angle = 90°, field of view (FOV) = 320 mm, acquired sequentially in an ascending direction. An automatic shimming procedure was performed before each scanning session. A total of 496 functional volumes were collected for each subject as well as high-resolution T1-weighted anatomical images (TE = 3.68 ms, TR = 2250 ms, slice thickness = 1 mm, 176 sagittal slices, FOV = 256 mm).

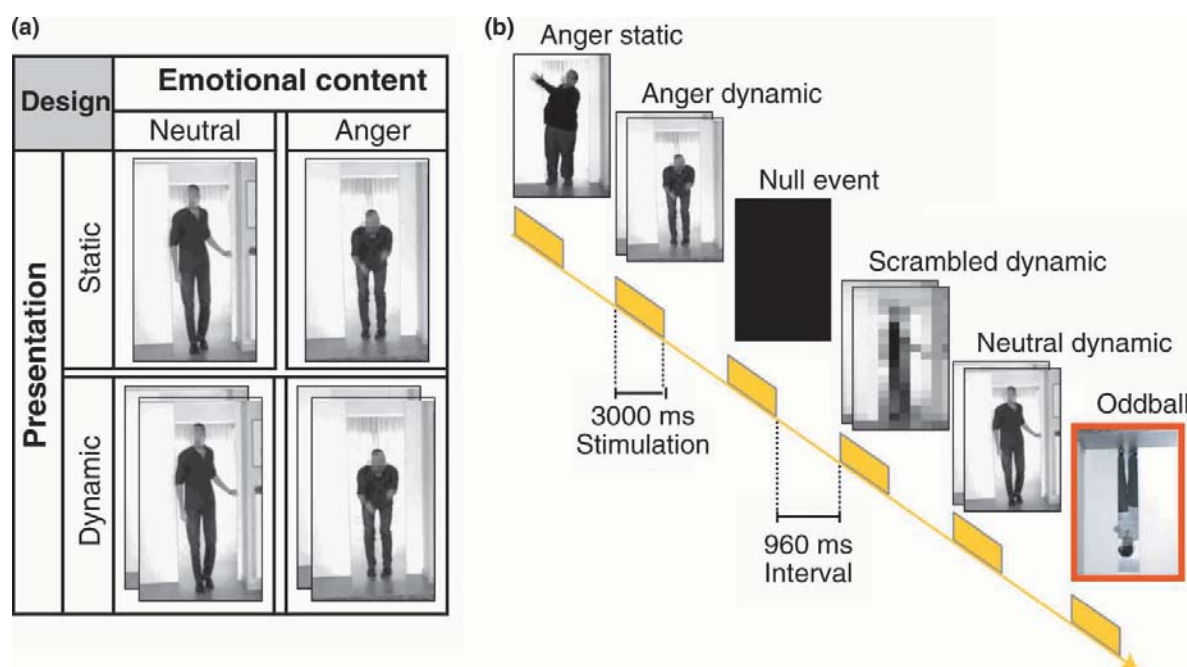


Figure 1. Experimental design and example of stimuli. (a) 2×2 factorial design. Trials were either movies or still pictures of whole-body expressions of actors opening a door in a neutral mode or angry mode. (b) Example of a run and timing. Participants were instructed to press a button when they saw an upside-down video clip among a run of body expressions (41% of the trials), scrambled (21%) and null (31%) stimuli. Targets were oddball (7%) trials. Stimuli were presented for 3 s, followed by a 960 ms long black screen.

fMRI data computation

Functional images were processed using the SPM2 software package (<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 491 functional images were reoriented to the AC–PC line, spatially realigned to the first volume by rigid body transformation and slice-time corrected to the middle slice. These images were normalized to the standard Montreal Neurological Institute (MNI) reference brain and subsampled at an isotropic voxel size of 2 mm. The normalized images were spatially smoothed by a 6 mm full width at half maximum (FWHM) isotropic Gaussian kernel.

Statistical analysis was carried out using the general linear model framework (Friston et al., 1995) implemented in the SPM2 software (SPM2; Wellcome Department of Imaging Neuroscience, London, UK). At the subject level, 7 effects of interest were modeled as follows: two represented the trials where subjects perceived body expressions of anger in a static (As) or dynamic way (Ad), two represented the trials where subjects perceived neutral body expressions in a static (Ns) or dynamic way (Nd). Finally, two represented the trials where subjects perceived scrambled static (Ss) or dynamic stimuli (Sd), and one represented the oddball stimuli. Null events were implicitly modeled. The BOLD response to the stimulus onset for each event type was convolved with the canonical hemodynamic 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 artifacts (the 3 rigid-body translations and the 3 rotations determined from initial spatial registration), and a single covariate representing the mean (constant) over scans. To remove low frequency drifts from the data, we applied a high-pass filter using a cut-off frequency of 1/128 Hz.

To implement a random effect analysis in SPM2, we first smoothed the images of parameter estimates of our 6 *t*-test contrasts of interest (As, Ad, Ns, Nd, Ss, Sd) using a 6 mm FWHM isotropic Gaussian kernel. Those images were then entered into a second-level analysis using within-subjects ANOVA with 6 hemodynamic response functions comprising a factor. A non-sphericity correction was applied for variance

differences between conditions and/or subjects. The following contrasts were calculated for the group:

- Main effect of bodies versus scrambled stimuli, $(As + Ad + Ns + Nd) - 2(Ss + Sd)$.
- Main effect of anger versus neutral bodies, $(As + Ad) - (Ns + Nd)$.
- Simple effect of anger dynamic versus anger static bodies, $(Ad - As)$.
- Simple effect of neutral dynamic versus neutral static bodies, $(Nd - Ns)$.
- Simple effect of anger dynamic versus neutral dynamic bodies, $(Ad - Nd)$.
- Interaction between anger and dynamic bodies, $(Ad - As) - (Nd - Ns)$.

All statistical parametric maps were thresholded at $p < .001$ (uncorrected for multiple comparisons), and activation foci with a minimum cluster extent of 10 voxels are reported here. Coordinates that survive False Discovery Rate (FDR) correction at $p < .05$ are indicated in tables by an asterisk. The maps were then overlaid on the MNI reference brain and labeled using the atlas of Duvernoy (1999). The reported coordinates in tables 2–5 represent peak activations of significant clusters except when their extent was important, in which case we also report subpeak coordinates corresponding to a different brain area from the maximum peak. For areas activated in both hemispheres, we report the coordinates of the strongest peak activation and provide both *Z*-values.

BEHAVIORAL RESULTS

After the scanning session, the participants performed a behavioral experiment. They viewed all 96 stimuli (24 static anger, 24 dynamic anger, 24 static neutral, 24 dynamic neutral) and were instructed to categorize each stimulus in a forced-choice procedure by pressing one of the two response buttons corresponding to the two emotional situations (anger or neutral). The average recognition rates for pictures and movies showing anger were respectively 80% ($SD = 16$) and 95% ($SD = 10$). The average recognition rates for neutral pictures and movies were respectively 90% ($SD = 9$) and 98% ($SD = 4$).

RESULTS

Effects of viewing body expressions irrespective of movement and emotion

The main effect of perceiving body expressions, irrespective of the movement properties and of the emotional content of the stimuli, (As+Ad+N_s+N_d) – 2(S_s+S_d) revealed significant increased activity in the amygdala, the fusiform gyrus, the middle occipital gyrus and the occipital pole in both hemispheres. In the right hemisphere, we observed activity in the pars orbitalis of the inferior frontal gyrus (BA 45) and the hippocampus. The full list of activations is presented in Table 2.

Effects of observing anger expressions irrespective of movement

The second analysis determined the activations specific to the presentation of anger expressions irrespective of the presence of movement in the stimuli by calculating the main effect of perceiving anger versus neutral body expressions: (As+Ad) – (Ns+N_d). This contrast revealed significant bilateral activations in the superior temporal sulcus (STS), the temporoparietal junction, the fusiform gyrus and the premotor cortex. In addition, in the right hemisphere there were significant activations in the amygdala, the thalamus, the medial part of the superior frontal gyrus (BA 9) and the pars triangularis of the inferior frontal gyrus (IFG, BA 45) extending onto the lateral OFC (BA 47). Loci in the left hemisphere

also included the lateral OFC (BA 47), the IFG (BA 45/BA 44) and the posterior cingulate sulcus. The full list of activations is presented in Table 3 (see Figure 2).

Effects of observing dynamic expressions

Data were then analyzed according to whether the images were dynamic or static by calculating the simple main effect of viewing dynamic versus static body expressions for anger (Ad–As) and for neutral (Nd–Ns) conditions separately. Neutral dynamic expressions elicited activity mainly located in the dorsal pathway whereas anger expressions recruited brain regions mainly located in the ventral pathway (see Figure 3a). Observing neutral dynamic expressions (Nd–Ns) is associated with bilateral activations in the MT/V5 complex, the posterior STS, the superior parietal lobe and the precuneus. In the right hemisphere, loci of activation were also detected in the fusiform gyrus and the premotor cortex. Observing angry dynamic expressions (Ad–As) elicited bilateral activations in the MT/V5 complex, the posterior STS, the fusiform gyrus, the temporal pole and the lateral OFC (see Figure 3a). Furthermore, in the right hemisphere, clusters of activity were detected along the STS extending to its anterior part as well as in the premotor cortex. In the left hemisphere, activations were elicited in the hypothalamus and the cerebellum. The full list of activations is presented in Table 4.

TABLE 2
Effects of observing body expressions versus scrambled stimuli (As+Ad+N_s+N_d) – 2(S_s+S_d)

Hemisphere	Anatomical region	MNI coordinates			Z-value	Cluster size
		x	y	z		
R	Inferior frontal gyrus-pars triangularis (BA 45)	56	30	–8	3.38*	10
L	Amygdala	–34	2	–24	3.64*	10
R	Amygdala	20	–2	–14	3.35*	38
R	Hippocampus	24	–24	–6	3.35*	65 [†]
R	Hippocampus	12	–32	–4	3.7*	65
R	Fusiform gyrus	42	–52	–20	Inf*	676
L	Fusiform gyrus	–40	–42	–22	5.26*	2988 [†]
R	Middle occipital gyrus	50	–76	0	Inf*	3410
L & R	Middle occipital gyrus	±44	–86	0	Inf*/7.73*	2988/3410 [†]
L & R	Occipital pole	±26	–100	–4	6.96*/7.28*	2988 [†] /3410 [†]

Notes: $p < .001$ uncorrected, * $p < .05$ FDR correction, minimum cluster extent = 10 voxels. Inf: Infinite. [†]for subpeaks.

TABLE 3
Main effect of anger versus neutral expressions (As+Ad)-(Ns+Nd)

Hemisphere	Anatomical region	MNI coordinates			Z-value	Cluster size
		x	y	z		
R	Superior frontal gyrus (BA 9)	10	60	40	4.54*	97
R	Inferior frontal gyrus (BA 45)/lateral orbitofrontal cortex (BA 47)	60	32	0	3.64*	93
L	Lateral orbitofrontal cortex (BA 47)	-42	30	-8	3.85*	26
L	Inferior frontal gyrus/sulcus (BA 45/BA 44)	-54	22	32	3.34*	12
L	Premotor cortex	-46	10	54	3.95*	27
R	Premotor cortex	42	2	44	4.30*	95
R	Amygdala	28	0	-26	3.84*	46
R	Thalamus	10	-12	6	3.53*	17
L	Posterior cingulate sulcus	-12	-6	42	3.57*	11
R	Superior temporal sulcus: middle part	54	-18	-14	3.78*	46
R	Temporoparietal junction-supramarginal gyrus	66	-34	36	3.61*	12
L & R	Temporoparietal junction-superior temporal gyrus	±66	-40	20	3.57*/4.92*	17/1343 [†]
L & R	Superior temporal sulcus: posterior part	±56	-42	4	5.55*/5.83*	1045/1343
L & R	Fusiform gyrus	±44	-44	-18	4.08*/4.68*	113/66
L & R	Middle occipital gyrus	±46	-74	0	5.27*/4.03*	1045 [†] /55
L & R	Occipital pole	±12	-102	2	5.30*/4.14*	540/79

Notes: $p < .001$ non-corrected. * $p < .05$ FDR correction, minimum cluster extent = 10 voxels. [†]for subpeaks.

Effects of observing dynamic expressions of anger

To identify brain activations specific to the perception of dynamic body expressions of anger, we calculated the interaction between the Presentation Mode (dynamic vs. static) and the factor Emotion (anger vs. neutral); (Ad-As)-(Nd-Ns). This contrast revealed significant bilateral activations in the lateral part of the temporal pole. In addition, in the right hemisphere, activations were detected all along the STS from its posterior ($y = -42$) to its anterior part ($y = -6$), in the anterior part of the ventromedial prefrontal cortex (gyrus rectus), in the dorsal premotor cortex and the superior frontal gyrus (BA 9). In the left hemisphere, significant hemodynamic responses were detected in the hypothalamus and in the medial part of the temporal pole. The full list of activations is given in Table 5 (see also Figure 4).

DISCUSSION

We investigated how the brain processes still images and short movies of actions involving the whole body and performed in a neutral or an angry fashion, and we show the condition-specific brain regions when participants view these stimuli. Perceiving body expressions of anger, whether static or dynamic, revealed activations in the amygdala, the fusiform gyrus, the lateral

OFC and the inferior frontal gyrus (BA 45). Additionally, perceiving anger movies specifically enhances activity in the hypothalamus, the temporal pole as well as the premotor and the ventromedial prefrontal cortex (vmPFC). Our discussion first addresses how seeing body expressions of anger influences activity in amygdala and within temporal cortices. We then consider whether these brain areas, in association with the lateral OFC, reflect an evaluation of emotional content. Finally, we highlight the possible involvement of the regions specifically recruited by the perception of movies of anger expressions in the modulation of autonomic reactions and motor responses known to be associated with defensive behavior.

Seeing anger stimuli activates the amygdala and fusiform gyrus

As predicted, the amygdala and the fusiform gyrus play a significant role in processing whole-body expressions of anger. To our knowledge this is the first report of amygdala activation triggered by the perception of whole-body expressions of anger. This new result extends previous findings that have already established the role of the amygdala in perceiving anger expressed in facial (see Table 1) and vocal expressions (Scott et al., 1997) as well as in actions involving body parts (Grosbras & Paus, 2006). The middle part of the

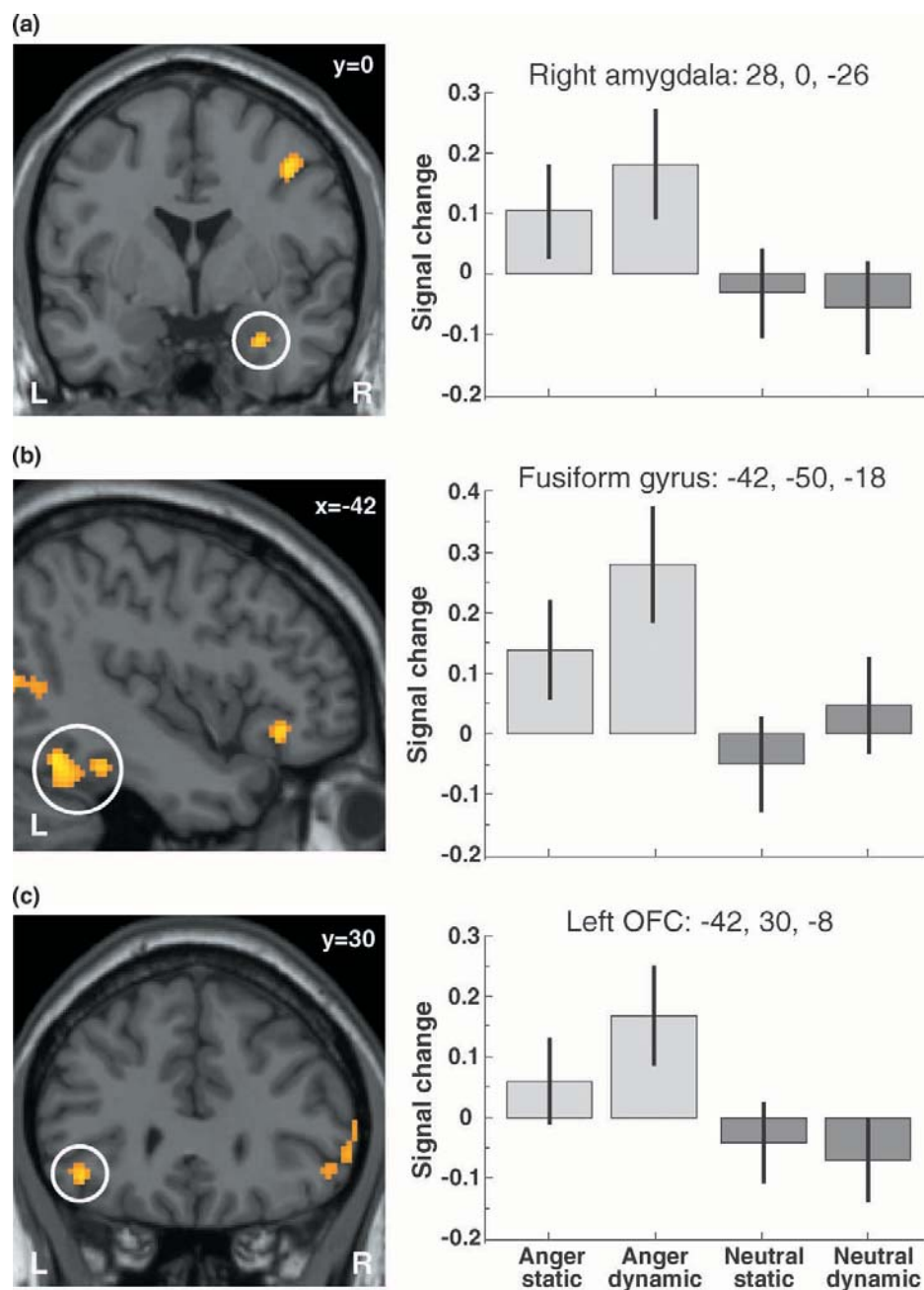


Figure 2. Regions showing amplitude difference when subjects observed static and dynamic expressions of anger. Localization of significant BOLD signal changes and parameter estimates (arbitrary units, mean centered) of the (a) right amygdala (b) left fusiform gyrus and (c) left OFC. Results superimposed on SPM standard single subject T1-weighted coronal and lateral sections, results listed in Table 3.

fusiform gyrus is associated with face perception but has also been associated with the processing of dynamic and static whole body movements and postures (Bonda, Petrides, Ostry, & Evans, 1996; Grossman & Blake, 2002; Kanwisher, Stanley, & Harris, 1999; Peelen & Downing, 2005; Vaina, Solomon, Chowdhury, Sinha, & Belliveau, 2001).

The observed involvement of amygdala and fusiform gyrus is also consistent with previous studies on body expressions of emotion using still images (de Gelder, Snyder, Greve, Gerard, & Hadjikhani, 2004; Grèzes, Pichon, & de Gelder, 2007; Hadjikhani & de Gelder, 2003). Recent fMRI studies using neutral faces and bodies have

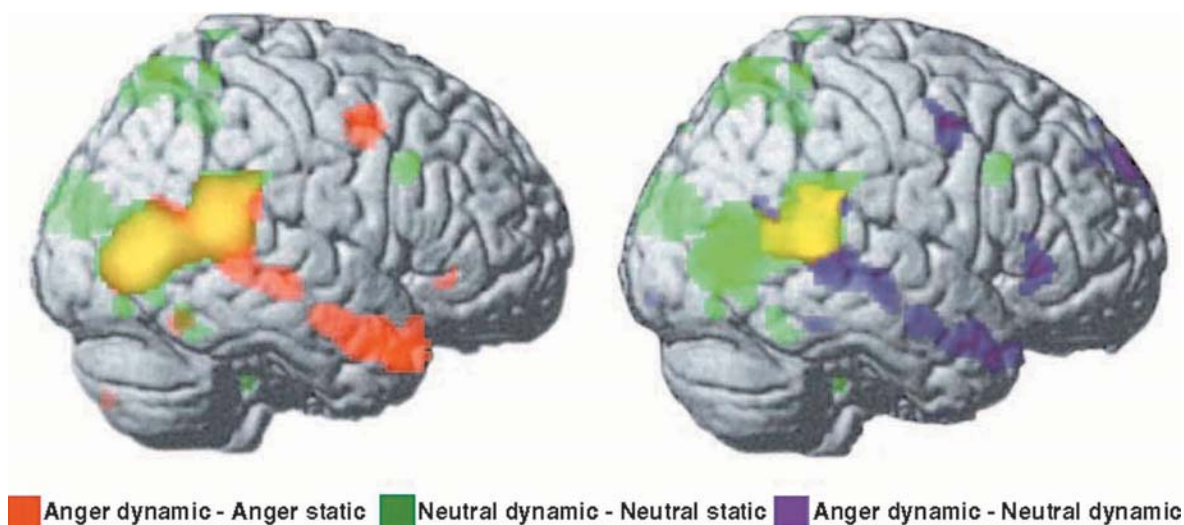


Figure 3. Cortical activations elicited by anger and neutral dynamic expressions. Statistical parametric maps ($p < .001$ uncorrected, minimum cluster extent of 10 voxels) of brain activation in response to the observation of (a) dynamic versus static anger expressions (red) and dynamic versus static neutral expressions (green) as well as (b) anger versus neutral dynamic expressions (purple). Common activations in both contrasts in yellow. Results listed in Table 4.

argued for a fine spatial segregation between the so-called body and face areas in the fusiform gyrus (Schwarzlose, Baker, & Kanwisher, 2005)

but also show a substantial overlap between them (Peelen, Wiggett, & Downing, 2006; van de Riet, Grèzes, & de Gelder, 2007).

TABLE 4
Brain regions involved during the observation of dynamic expressions (Ad-As)/(Nd-Ns)

Hemi- sphere	Anatomical region	MNI coordinates			Z-value	Cluster size
		x	y	z		
<i>Dynamic vs. static anger expressions (Ad-As)</i>						
L & R	Lateral orbitofrontal cortex (BA 47)	±38	30	0	3.56*/3.35*	10/11
L & R	Temporal pole: medial part	±28	12	-30	3.50*/3.70*	13/33
R	Middle temporal gyrus: anterior part	54	8	-22	4.75*	562 [†]
L	Hypothalamus	-6	0	-14	3.45*	12
R	Premotor cortex	50	2	48	4.35*	130
R	Superior temporal sulcus: anterior part (aSTS)	54	-2	-24	5.02*	562
R	Temporoparietal junction (TPJ)	68	-38	22	5.51*	2972 [†]
L & R	Fusiform gyrus	±42	-42	-20	3.88*/3.60*	52/17
L & R	Superior temporal sulcus: posterior part	±54	-44	12	5.88*/7.65*	1343 [†] /2972 [†]
L & R	Middle occipital gyrus (MT/V5)	±48	-68	4	7.68*/Inf*	1343/2972
L	Cerebellum	-12	-80	-46	3.5*	15
<i>Dynamic vs. static neutral expressions (Nd-Ns)</i>						
R	Inferior frontal gyrus (BA 44)	52	16	32	3.61*	56
L & R	Intraparietal/postcentral sulcus	±42	-46	62	3.56*/3.54*	15/33
L & R	Superior temporal sulcus: posterior part	±62	-44	16	4.68*/6.71*	1488 [†] /2790 [†]
L & R	Precuneus	±8	-74	56	3.51*/3.24*	21/14
R	Precuneus	8	-50	50	4.69*	115
L	Superior parietal lobule/intraparietal sulcus	-34	-62	52	4.34*	254
R	Superior parietal lobule	26	-66	66	4.22*	225
R	Fusiform gyrus	42	-56	-18	3.86*	36
L & R	Middle occipital gyrus (MT/V5)	±48	-70	2	Inf*/Inf*	1488/2790
L & R	Superior occipital gyrus	±24	-94	24	4.77*/3.97*	348/163
L & R	Occipital gyrus	±46	-76	-14	3.37*/3.65*	14/2790 [†]

Notes: $p < .001$ non-corrected. * $p < .05$ FDR correction, minimum cluster extent = 10 voxels, Inf: Infinite, [†]for subpeaks.

TABLE 5

Brain regions specifically involved during the observation of dynamic expressions of anger revealed by the interaction (Ad-As)-(Nd-Ns)

Hemisphere	Anatomical region	MNI coordinates			Z-value	Cluster size
		x	y	z		
R	Superior frontal gyrus (BA 9)	6	56	48	3.35	10
R	Ventromedial prefrontal cortex/gyrus rectus	2	48	-26	3.53	25
R	Premotor cortex (PM): dorsal part	56	-4	52	3.62	22
L	Hypothalamus	-6	0	-12	4.24	53
R	Superior temporal sulcus: posterior part	48	-42	8	3.49	37
R	Superior temporal sulcus: middle part	54	-22	-6	3.84	31
R	Superior temporal sulcus: anterior part	54	-6	-20	3.87	80
L & R	Temporal pole: lateral part	±54	14	-26	3.98/3.83	29/72
L	Temporal pole: medial part	-32	12	-30	3.85	25

Notes: $p < .001$ uncorrected, minimum cluster extent = 10 voxels.

Our results provide support for the hypothesis that the amygdala plays a major role in detecting threat and add to the significant literature on the contribution of the amygdala to the perception of fear and the brain's response to threat (Anderson & Phelps, 2000; LeDoux, 2000). The combined activation of the amygdala and fusiform gyrus triggered by anger in body actions is also consistent with functional data from healthy subjects (Morris et al., 1998), findings with brain-injured patients (Vuilleumier, Richardson, Armony, Driver, & Dolan, 2004) and tracing studies in animals showing massive projections from the amygdala to all levels of the ventral visual pathway (Amaral, Behniea, & Kelly, 2003), which suggests that the amygdala can influence sensory processing in the fusiform gyrus. It also extends the previously observed activations in the amygdala and fusiform for fear body actions (de Gelder et al., 2004; Hadjikhani & de Gelder, 2003; Grèzes et al., 2007) by showing that the amygdala's reaction to threat in anger stimuli is combined with activity in the fusiform gyrus.

Anger-related activations and the lateral OFC

In addition to the amygdala and fusiform gyrus, we observed activation in the inferior frontal gyrus and lateral OFC in response to anger expressions. Previous neuroimaging findings that have used facial expressions of anger have frequently reported enhanced activity in the lateral OFC (see Table 1). Besides anger, this region was also detected during the perception of an emotional tone of voice (Wildgruber et al.,

2004, 2005) and facial expressions (Nakamura et al., 1999). In keeping with this, patients with OFC lesions are impaired at recognizing that actions leading to social violation are inappropriate (Hornak, Rolls, & Wade, 1996). Interestingly, the lateral OFC is also active in healthy subjects judging scenarios describing transgressions of social norms (Berthoz, Armony, Blair, & Dolan, 2002). When combining these results it seems that the brain areas activated in the main effect of body expressions of anger may be linked to the integration of emotion-related information and processes assigning affective meaning to the stimuli.

Perception of dynamic body expressions of anger and neural substrate

In addition to brain areas responding to body images of anger irrespective of whether the information is provided by videos or still images, the interaction revealed regions specifically activated in response to dynamic expressions of anger. These include the temporal pole, which is the site of convergence of sensory and limbic inputs (Moran, Mufson, & Mesulam, 1987) and has an important role in affective processes (Adolphs, Tranel, & Damasio, 2001; Anderson & Phelps, 2000). Our analysis also reveals the hypothalamus, the vmPFC and the premotor cortex (see Figure 4). The hypothalamus is known to play a key role in regulating autonomic systems as well as in sustaining complex behavioral responses. Electrical stimulation of the hypothalamus induces typical defensive reactions in

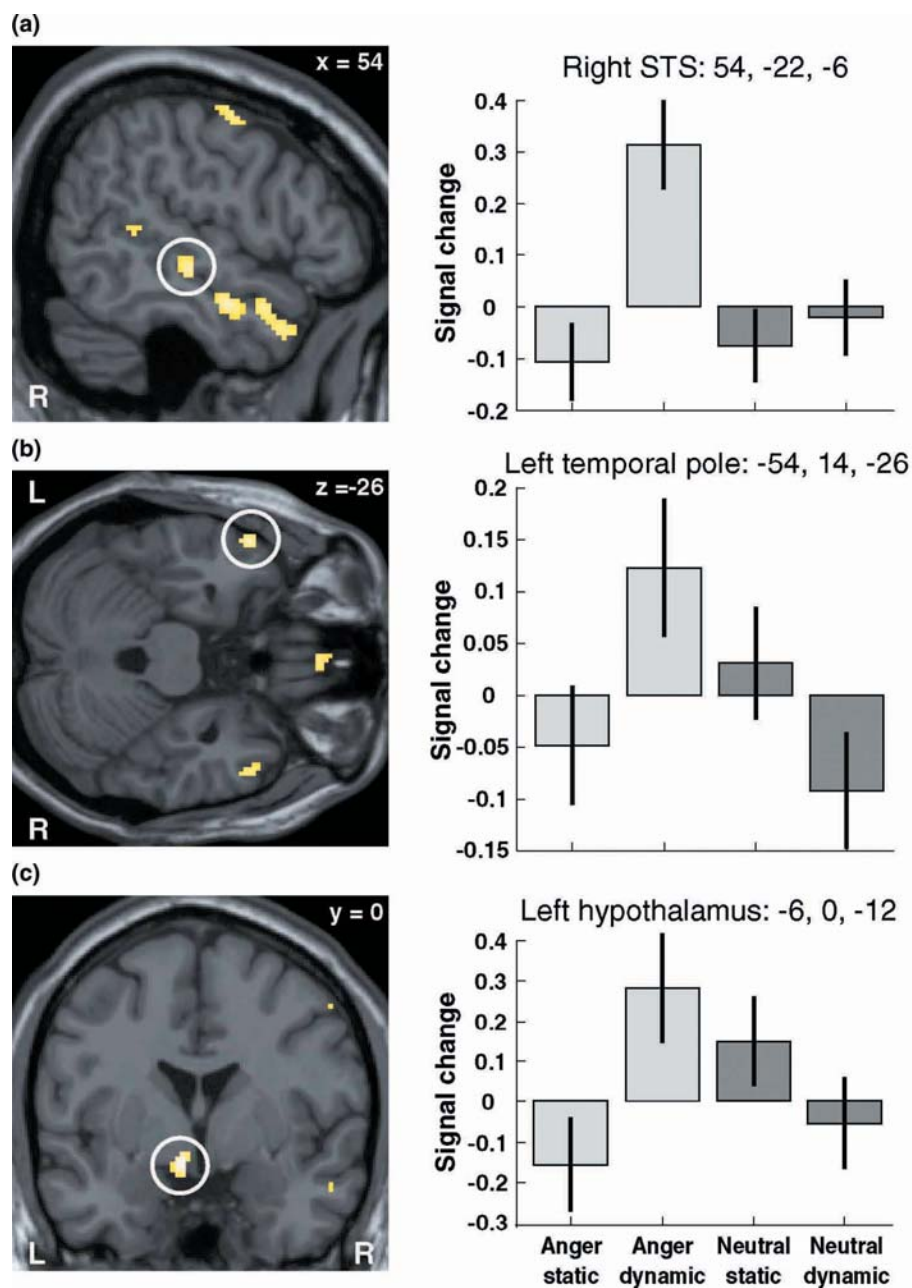


Figure 4. Regions showing amplitude difference when subjects observed dynamic expressions of anger revealed by the interaction. Localization of significant BOLD signal changes and parameter estimates (arbitrary units, mean centered) of the (a) right STS (b) left temporal pole and (c) left hypothalamus. Results superimposed on SPM standard single subject T1-weighted sagittal, axial and coronal sections, results listed in Table 5.

animals (Hess & Akert, 1955) ranging from stereotypical flight to attack (Brown, Hunsperger, & Rosvold, 1969), and aggressive reactions in humans (Bejjani et al., 2002), suggesting that the hypothalamus plays a role in emotional processes by preparing the body for action. Moreover, it was also shown to be elicited during the recall of

autobiographic emotional memories (Damasio et al., 2000).

The vmPFC has massive direct excitatory projections onto the hypothalamus (Ongur, An, & Price, 1998) and was suggested to be involved in the regulation of social and aggressive behaviors (Blair, 2004; Damasio, 1994; Davidson, Putnam,

& Larson, 2000). Patients with vmPFC lesions have behavioral impairments characterized by poor personal decision making and inappropriate social behavior (Bechara, Damasio, Damasio, & Anderson, 1994; Grafman et al., 1996). Also, OFC lesions result in difficulties in re-experiencing emotion from internally generated images of emotional situations as reflected by low physiological activity and low subjective rating of feeling the emotion (Bechara, Damasio, & Damasio, 2003). Together with the amygdala, the temporal pole and the hypothalamus, the vmPFC is part of a tightly connected anatomical network in the rhesus monkey (Barbas, Saha, Rempel-Clower, & Ghashghaei, 2003; Ongur & Price, 2000) that appears preferentially linked with the expression of emotional responses by exerting a direct control on autonomic activity in response to threatening stimuli. Against this background, an explanation for the recruitment of this network may be that responding to dynamic signals of anger modulates the activity of neural structures that are involved in the elaboration of autonomic and defensive responses.

Finally, the perception of dynamic body expressions of anger is also associated with specific increased hemodynamic activity in the dorsal premotor cortex. This activation may reflect preparation for action. This interpretation is supported by significant differences in premotor activity when the perception of anger is contrasted to the perception of fearful static facial expressions (Whalen et al., 2001) and by the fact that, in the present study, angry actions clearly involve the precentral gyrus in its dorsal part ($z = 52$), whereas neutral actions elicit activity in the dorsal part of Broca area 44 (see Figure 3). The dorsal premotor cortex is known to be implicated in motor preparation and environmentally triggered actions (Hoshi & Tanji, 2004; Passingham, 1993). Finally, the possibility that activity in the premotor cortex may reflect preparation for action is also supported by the presence of activity in subcortical nuclei, e.g., hypothalamus and amygdala, in response to anger expressions. Subcortical structures such as the periaqueductal grey, hypothalamus and amygdala play an important role in organizing defensive reactions (Panksepp, 1998) and there is evidence of direct projections from the hypothalamus to the amygdala's basal nucleus (Barbas et al., 2003) that projects to the premotor cortex (Avendano, Price, & Amaral, 1983). Interestingly, stimulation of a polysensory zone in the precentral gyrus

elicits reflexive protective movements in monkeys (Graziano & Cooke, 2006).

CONCLUSION

We show that viewing whole-body expressions of anger elicits activity in amygdala and fusiform gyres indicating detection and associated modulation of visual cortical areas. Furthermore, taking into account equally strong activation in the lateral OFC, we submit that the activity in these areas may reflect the evaluation of emotionally laden stimuli and a reaction to threat emanating from the anger expressed in the bodies. Strikingly, we observed that anger movies additionally activate visceromotor areas such as the hypothalamus, the premotor cortex, and the ventromedial prefrontal cortex, which are involved in the elaboration of autonomic and defensive reactions. Our results provide novel insights into the neural substrates of emotion and adaptive action in the face of social threat. They also underscore the importance of using stimuli consisting of emotional expressions by the entire body including biological movement in future neuroimaging investigations of emotional processes.

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REFERENCES

- Adolphs, R., Tranel, D., & Damasio, H. (2001). Emotion recognition from faces and prosody following temporal lobectomy. *Neuropsychology*, *15*, 396–404.
- Amaral, D. G. (2003). The amygdala, social behavior, and danger detection. *Annals of the New York Academy of Sciences*, *1000*, 337–347.
- Amaral, D. G., Behniea, H., & Kelly, J. L. (2003). Topographic organization of projections from the amygdala to the visual cortex in the macaque monkey. *Neuroscience*, *118*, 1099–1120.
- Anderson, A. K., & Phelps, E. A. (2000). Expression without recognition: Contributions of the human amygdala to emotional communication. *Psychological Science*, *11*, 106–111.
- Argyle, M. (1988). *Bodily communication* (2nd ed.). New York: Methuen.
- 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*, 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 Research*, 264, 111–117.
- Barbas, H., Saha, S., Rempel-Clower, N., & Ghashghaei, H. T. (2003). Serial pathways from primate prefrontal cortex to autonomic areas may influence emotional expression. *BMC Neuroscience*, 4, 25.
- Bechara, A., Damasio, A. R., Damasio, H., & Anderson, S. W. (1994). Insensitivity to future consequences following damage to human prefrontal cortex. *Cognition*, 50, 7–15.
- Bechara, A., Damasio, H., & Damasio, A. R. (2003). Role of the amygdala in decision-making. *Annals of the New York Academy of Sciences*, 985, 356–369.
- Bejjani, B. P., Houeto, J. L., Hariz, M., Yelnik, J., Mesnage, V., Bonnet, A. M., et al. (2002). Aggressive behavior induced by intraoperative stimulation in the triangle of Sano. *Neurology*, 59, 1425–1427.
- Berthoz, S., Armony, J. L., Blair, R. J., & Dolan, R. J. (2002). An fMRI study of intentional and unintentional (embarrassing) violations of social norms. *Brain*, 125, 1696–1708.
- Blair, R. J. R. (2004). The roles of orbital frontal cortex in the modulation of antisocial behavior. *Brain and Cognition*, 55, 198–208.
- Blair, R. J. R., 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, 883–893.
- Blanchard, D. C., & Blanchard, R. J. (1972). Innate and conditioned reactions to threat in rats with amygdaloid lesions. *Journal of Comparative and Physiological Psychology*, 81, 281–190.
- Blanchard, D. C., & Blanchard, R. J. (1988). Ethoexperimental approaches to the biology of emotion. *Annual Review of Psychology*, 39, 43–68.
- Bonda, E., Petrides, M., Ostry, D., & Evans, A. (1996). Specific involvement of human parietal systems and the amygdala in the perception of biological motion. *Journal of Neuroscience*, 16, 3737–3744.
- Brown, J. L., Hunzinger, R. W., & Rosvold, H. E. (1969). Defence, attack, and flight elicited by electrical stimulation of the hypothalamus of the cat. *Experimental Brain Research*, 8, 113–129.
- Damasio, A. R. (1994). *Descartes' error: Emotion, rationality and the human brain*. New York: Grosset/Putnam.
- Damasio, A. R., Grabowski, T. J., Bechara, A., Damasio, H., Ponto, L. L., Parvizi, J., et al. (2000). Subcortical and cortical brain activity during the feeling of self-generated emotions. *Nature Neuroscience*, 3, 1049–1056.
- Davidson, R. J., Putnam, K. M., & Larson, C. L. (2000). Dysfunction in the neural circuitry of emotion regulation—a possible prelude to violence. *Science*, 289, 591–594.
- de Gelder, B. (2006). Towards the neurobiology of emotional body language. *Nature Reviews Neuroscience*, 7, 242–249.
- 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. *Proceedings of the National Academy of Sciences of the USA*, 101, 16701–16706.
- de Meijer, M. (1989). The contribution of general features of body movement to the attribution of emotions. *Journal of Nonverbal Behavior*, 13, 247–268.
- Decety, J., & Chaminade, T. (2003). Neural correlates of feeling sympathy. *Neuropsychologia*, 41, 127–138.
- Dimberg, U. (1986). Facial expressions as excitatory and inhibitory stimuli for conditioned autonomic responses. *Biological Psychology*, 22, 37–57.
- Duvernoy, H. M. (1999). *The human brain: Surface, three-dimensional sectional anatomy with MRI, and blood supply*. Vienna: Springer-Verlag.
- Emery, N. J., & Amaral, D. G. (2000). The role of the amygdala in primate social cognition. In R.D. Lane & L. Nadel (Eds.) *Cognitive neuroscience of emotion* (pp. 156–191). New York University Press.
- Esslen, M., Pascual-Marqui, R. D., Hell, D., Kochi, K., & Lehmann, D. (2004). Brain areas and time course of emotional processing. *NeuroImage*, 21, 1189–1203.
- Fitzgerald, D. A., Angstadt, M., Jelsone, L. M., Nathan, P. J., & Phan, K. L. (2006). Beyond threat: amygdala reactivity across multiple expressions of facial affect. *NeuroImage*, 30, 1441–1448.
- Frijda, N. H. (1986). *The emotions*. Cambridge, UK: Cambridge University Press.
- Friston, K. J., Holmes, A. P., Worsley, K. J., Poline, J. B., Frith, C. D., & Frackowiak, R. S. J. (1995). Statistical parametric maps in functional imaging: a general linear approach. *Human Brain Mapping*, 2, 189–210.
- Grafman, J., Schwab, K., Warden, D., Pridgen, A., Brown, H. R., & Salazar, A. M. (1996). Frontal lobe injuries, violence, and aggression: a report of the Vietnam Head Injury Study. *Neurology*, 46, 1231–1238.
- Graziano, M. S., & Cooke, D. F. (2006). Parieto-frontal interactions, personal space, and defensive behavior. *Neuropsychologia*, 44, 845–859.
- Grèzes, J., Pichon, S., & de Gelder, B. (2007). Perceiving fear in dynamic body expressions. *NeuroImage*, 35, 959–967.
- Grosbras, M. H., & Paus, T. (2006). Brain networks involved in viewing angry hands or faces. *Cerebral Cortex*, 16, 1087–1096.
- Grossman, E., & Blake, R. (2002). Brain areas active during visual perception of biological motion. *Neuron*, 35, 1167–1175.
- Hadjikhani, N., & de Gelder, B. (2003). Seeing fearful body expressions activates the fusiform cortex and amygdala. *Current Biology*, 13, 2201–2205.
- Hennenlotter, A., & Schroeder, U. (2006). Partly dissociable neural substrates for recognizing basic emotions: a critical review. *Progress in Brain Research*, 156, 433–456.
- Hess, W. R., & Akert, K. (1955). Experimental data on role of hypothalamus in mechanism of emotional behavior. *AMA Archives of Neurology and Psychiatry*, 73, 127–129.
- Hornak, J., Rolls, E. T., & Wade, D. (1996). Face and voice expression identification in patients with emotional and behavioural changes following ventral frontal lobe damage. *Neuropsychologia*, 34, 247–261.

- Hoshi, E., & Tanji, J. (2004). Functional specialization in dorsal and ventral premotor areas. *Progress in Brain Research*, *143*, 507–511.
- Kanwisher, N., Stanley, D., & Harris, A. (1999). The fusiform face area is selective for faces not animals. *Neuroreport*, *10*, 183–187.
- Kesler-West, M. L., Andersen, A. H., Smith, C. D., Avison, M. J., Davis, C. E., Kryscio, R. J., et al. (2001). Neural substrates of facial emotion processing using fMRI. *Brain Research Cognitive Brain Research*, *11*, 213–226.
- Kilts, C. D., Egan, G., Gideon, D. A., Ely, T. D., & Hoffman, J. M. (2003). Dissociable neural pathways are involved in the recognition of emotion in static and dynamic facial expressions. *NeuroImage*, *18*, 156–168.
- LaBar, K. S., Crupain, M. J., Voyvodic, J. T., & McCarthy, G. (2003). Dynamic perception of facial affect and identity in the human brain. *Cerebral Cortex*, *13*, 1023–1033.
- LeDoux, J. E. (2000). Emotion circuits in the brain. *Annual Review of Neuroscience*, *23*, 155–184.
- McNaughton, N., & Corr, P. J. (2004). A two-dimensional neuropsychology of defense: fear/anxiety and defensive distance. *Neuroscience and Biobehavioral Reviews*, *28*, 285–305.
- Moran, M. A., Mufson, E. J., & Mesulam, M. M. (1987). Neural inputs into the temporopolar cortex of the rhesus monkey. *Journal of Comparative Neurology*, *256*, 88–103.
- Morris, J. S., Friston, K. J., Buchel, C., Frith, C. D., Young, A. W., Calder, A. J., et al. (1998). A neuromodulatory role for the human amygdala in processing emotional facial expressions. *Brain*, *121*, 47–57.
- Murphy, F. C., Nimmo-Smith, I., & Lawrence, A. D. (2003). Functional neuroanatomy of emotions: a meta-analysis. *Cognitive, Affective & Behavioral Neuroscience*, *3*, 207–233.
- Nakamura, K., Kawashima, R., Ito, K., Sugiura, M., Kato, T., Nakamura, A., et al. (1999). Activation of the right inferior frontal cortex during assessment of facial emotion. *Journal of Neurophysiology*, *82*, 1610–1614.
- Ongur, D., An, X., & Price, J. L. (1998). Prefrontal cortical projections to the hypothalamus in macaque monkeys. *Journal of Comparative Neurology*, *401*, 480–505.
- Ongur, D., & Price, J. L. (2000). The organization of networks within the orbital and medial prefrontal cortex of rats, monkeys and humans. *Cerebral Cortex*, *10*, 206–219.
- Panksepp, J. (1998). *Affective neuroscience: The foundation of human and animal emotions*. New York: Oxford University Press.
- Passingham, R. E. (1993). *The frontal lobes and voluntary action*. Oxford: Oxford University Press.
- Peelen, M. V., & Downing, P. E. (2005). Selectivity for the human body in the fusiform gyrus. *Journal of Neurophysiology*, *93*, 603–608.
- Peelen, M. V., Wiggett, A. J., & Downing, P. E. (2006). Patterns of fMRI activity dissociate overlapping functional brain areas that respond to biological motion. *Neuron*, *49*, 815–822.
- 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 Research Cognitive Brain Research*, *20*, 81–91.
- Schupp, H. T., Ohman, A., Junghofer, M., Weike, A. I., Stockburger, J., & Hamm, A. O. (2004). The facilitated processing of threatening faces: an ERP analysis. *Emotion*, *4*, 189–200.
- Schwarzlose, R. F., Baker, C. I., & Kanwisher, N. (2005). Separate face and body selectivity on the fusiform gyrus. *Journal of Neuroscience*, *25*, 11055–11059.
- Scott, S. K., Young, A. W., Calder, A. J., Hellawell, D. J., Aggleton, J. P., & Johnson, M. (1997). Impaired auditory recognition of fear and anger following bilateral amygdala lesions. *Nature*, *385*, 254–257.
- Simon, D., Craig, K. D., Miltner, W. H. R., & Rainville, P. (2006). Brain responses to dynamic facial expressions of pain. *Pain*, *126*, 309–318.
- Sprengelmeyer, R., Rausch, M., Eysel, U. T., & Przuntek, H. (1998). Neural structures associated with recognition of facial expressions of basic emotions. *Proceedings: Biological Sciences*, *265*, 1927–1931.
- Strauss, M. M., Makris, N., Aharon, I., Vangel, M. G., Goodman, J., Kennedy, D. N., et al. (2005). fMRI of sensitization to angry faces. *NeuroImage*, *26*, 389–413.
- Vaina, L. M., Solomon, J., Chowdhury, S., Sinha, P., & Belliveau, J. W. (2001). Functional neuroanatomy of biological motion perception in humans. *Proceedings of the National Academy of Sciences of the USA*, *98*, 11656–11661.
- van de Riet, W. A., Grèzes, J., & de Gelder, B. (2007). Neural correlates of perceiving the facial and the bodily expression simultaneously. *Human Brain Mapping*, Abstract.
- Vuilleumier, P., Richardson, M. P., Armony, J. L., Driver, J., & Dolan, R. J. (2004). Distant influences of amygdala lesion on visual cortical activation during emotional face processing. *Nature Neuroscience*, *7*, 1271–1278.
- 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*, 70–83.
- Wildgruber, D., Hertrich, I., Riecker, A., Erb, M., Anders, S., Grodd, W., et al. (2004). Distinct frontal regions subserve evaluation of linguistic and emotional aspects of speech intonation. *Cerebral Cortex*, *14*, 1384–1389.
- Wildgruber, D., Riecker, A., Hertrich, I., Erb, M., Grodd, W., Ethofer, T., et al. (2005). Identification of emotional intonation evaluated by fMRI. *NeuroImage*, *24*, 1233–1241.
- Williams, L. M., Brown, K. J., Das, P., Boucsein, W., Sokolov, E. N., Brammer, M. J., et al. (2004). The dynamics of cortico-amygdala and autonomic activity over the experimental time course of fear perception. *Cognitive Brain Research*, *21*, 114–123.