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Publisher Psychology Press

Informa Ltd Registered in England and Wales Registered Number: 1072954 Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK



Social Neuroscience

Publication details, including instructions for authors and subscription information:

<http://www.informaworld.com/smpp/title~content=t741771143>

Specific and common brain regions involved in the perception of faces and bodies and the representation of their emotional expressions

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Online Publication Date: 01 April 2009

To cite this Article van de Riet, Wim A. C., Grèzes, Julie and de Gelder, Beatrice(2009)'Specific and common brain regions involved in the perception of faces and bodies and the representation of their emotional expressions',*Social Neuroscience*,4:2,101 — 120

To link to this Article: DOI: 10.1080/17470910701865367

URL: <http://dx.doi.org/10.1080/17470910701865367>

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Specific and common brain regions involved in the perception of faces and bodies and the representation of their emotional expressions

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Many studies provide support for the role of the fusiform gyrus in face recognition and its sensitivity to emotional expressions. Recently, category-specific representation was also observed for neutral human bodies in the middle temporal/middle occipital gyrus (extrastriate body area) but it is not clear whether this area is also sensitive to emotional bodily expressions. Besides these areas, other regions that process the affective information carried by the face and the body may be common and/or specific to the face or the body. To clarify these issues we performed a systematic comparison of how the whole brain processes faces and bodies and how their affective information is represented. Participants categorized emotional facial and bodily expressions while brain activity was measured using functional magnetic resonance imaging. Our results show that, first, the amygdala and the fusiform gyrus are sensitive to recognition of facial and bodily fear signals. Secondly, the extrastriate body area–area V5/MT is specifically involved in processing bodies without being sensitive to the emotion displayed. Thirdly, other important areas such as the superior temporal sulcus, the parietal lobe and subcortical structures represent selectively facial and bodily expressions. Finally, some face/body differences in activation are a function of the emotion expressed.

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We are grateful to I. Toni for advice on the design of the study, M. Barth for advice on the scanning parameters, P. Gaalman, R. Scheeringa and R. B. Mars for technical assistance, H. K. M. Meeren for assistance with the stimulus presentation programming, S. van der Goor and R. A. Otte for their assistance with the stimulus preparation and with the validation of the stimuli, S. Pichon for advice on the fMRI analysis, and R. Righart, J. Van den Stock and B. M. C. Stienen for comments on the manuscript. The authors were partly supported by Human Frontier Science Program HFSP-RGP0054/2004-C.

Faces appear to occupy a unique position by virtue of the fact that they provide many highly relevant cues about the identity, emotional states and social intentions of the persons encountered. The neuroimaging studies of Sergent and Signoret (1992) and Haxby et al. (1994) have drawn attention to the middle part of the fusiform gyrus as the putative anatomical locus underlying face recognition, a region later dubbed the fusiform face area (Kanwisher, McDermott, & Chun, 1997). Other relevant areas have received less attention but are probably at least as important for understanding the functional aspects of face representation in the brain. Face sensitivity has been reported for the inferior occipital gyrus (Gauthier, Skudlarski, Gore, & Anderson, 2000; Puce, Allison, Asgari, Gore, & McCarthy, 1996) and the superior temporal sulcus (Kanwisher et al., 1997). So far the exact functional connections between these major face areas, their sensitivity to the perceptual task at hand, and the role they play in processing the emotional expression are issues that are not clear.

This is important in view of the fact that faces are not the only bearers of emotional messages. The human body as a whole, to which the face belongs, is a powerful conveyer of emotional signals and emotion-related action intentions. Depending on whether the emphasis is on the visual object categories or on how both can convey the same meaning, one may either stress the differences between faces and bodies as visual objects or underscore their similarity as emotional signals. In the present study our interest lies with the latter perspective.

Recent neuroimaging studies indicate that the human body may also represent a special perceptual category. Downing, Jiang, Shuman, and Kanwisher (2001) reported that a region in the middle temporal and middle occipital gyrus, which they labeled the extrastriate body area, was sensitive to body parts and whole bodies, a finding replicated in later studies using body stimuli (Grossman & Blake, 2002; Peelen & Downing, 2005; Sakreida, Schubotz, Wolfensteller, & von Cramon, 2005; Spiridon, Fischl, & Kanwisher, 2006). Studies of category-specificity reported body-specific processing not only in the extrastriate body area but also in the fusiform gyrus (Peelen and Downing, 2005; Schwarzlose, Baker, & Kanwisher, 2005; Spiridon et al., 2006). Peelen and Downing (2005) and Schwarzlose et al. (2005), using higher resolution techniques,

argue for a spatial segregation between the spatially close cortical areas for faces vs. bodies and for a separate fusiform face and fusiform body area, a notion elaborated and statistically tested by Peelen, Wiggett, and Downing (2006) with multivoxel pattern analysis.

Investigations of category-specific brain areas typically rely on cross-category comparisons, mainly contrasting faces with objects (e.g., Henson et al., 2003; Kanwisher et al., 1997; Spiridon et al., 2006) or faces and bodies with tools (Peelen & Downing, 2005). But how does the presence of the same attribute affect category boundaries? So far this question was almost exclusively addressed for the selectivity of the fusiform gyrus for faces and for faces expressing fear. Other face- or body-sensitive areas and other emotions were not taken into account (but see Grosbras & Paus, 2006). Convergent results show that the presence of a facial expression increases activation in the fusiform gyrus (Dolan, Morris, & de Gelder, 2001; Morris, Öhman, & Dolan, 1998; Rotshtein, Malach, Hadar, Graif, & Hendler, 2001). To explain this increase, a mechanism of feedback from the amygdala to the fusiform gyrus was originally suggested (Breiter et al., 1996; Morris et al., 1998; Sugase, Yamane, Ueno, & Kawano, 1999). Support for this hypothesis comes from findings that patients with amygdala lesions are impaired in their recognition of facial expressions (Adolphs, Tranel, Damasio, & Damasio, 1994, 1995; Adolphs et al., 1999; Young et al., 1995; Young, Hellawell, Van De Wal, & Johnson, 1996). Also, in patients with amygdala lesions activity in the fusiform gyrus was not enhanced when fearful and neutral facial expressions were shown (Vuilleumier, Richardson, Armony, Driver, & Dolan, 2004).

A similar argument has been advanced to explain the increased activation level for fearful compared to neutral body expressions based on the finding that observing fearful bodies with faces blurred increases activity in the amygdala and the fusiform gyrus (de Gelder, Snyder, Greve, Gerard, & Hadjikhani, 2004; Hadjikhani & de Gelder, 2003). In contrast to the prominent fusiform gyrus activation, the latter two studies did not find evidence for the involvement of the extrastriate body area. We conjectured that since all conditions included body stimuli, no body-specific area such as the extrastriate body area would have emerged in the analysis (de Gelder et al., 2004). This explanation implies that the

extrastriate body area is not differentially sensitive to the fearful, happy or neutral body conditions used. Taken together the evidence suggests that the fusiform gyrus is sensitive to facial expressions, to bodies and to the emotion they convey, while the extrastriate body area only implements processing the body shape. But this conclusion is achieved at the price of combining results across different studies, methods and tasks. What is needed at present is a systematic comparison of the brain representation of faces and bodies, with and without emotional expression. It is advisable not to focus on the role of face and body areas narrowly conceived because other regions besides the fusiform gyrus are known to reflect the specific influence of the affective component present in faces and bodies. Some of these are known already to be relevant for processing the affective component of faces, such as the superior temporal sulcus, which figures in distributed models of face processing (Adolphs, 2002; de Gelder, Frissen, Barton, & Hadjikhani, 2003; de Gelder & Rouw, 2001; de Gelder et al., 2004; Grèzes, Pichon, & de Gelder, 2007; Haxby, Hoffman, & Gobbini, 2000) and is often linked to processing emotional expressions in the face, processing social information and to biological movement perception (Allison, Puce, & McCarthy, 2000; Baylis, Rolls, & Leonard, 1985; Bruce, Desimone, & Gross, 1981; Mikami, Nakamura, & Kubota, 1994; Perrett, Rolls, & Caan, 1982; Perrett et al., 1985; Pichon, de Gelder, & Grèzes, in press; Rolls, Baylis, & Hasselmo, 1987).

Other regions of importance are the insula, the orbitofrontal cortex and the primary somatosensory cortex. They are involved in the processing of emotional facial and/or bodily expressions (Adolphs, 2002; Adolphs, Damasio, Tranel, Cooper, & Damasio, 2000; de Gelder, 2006; de Gelder et al., 2004; Wright, He, Shapira, Goodman, & Liu, 2004) and comprise, together with the abovementioned areas, a network devoted to the processing of face and body and their respective emotion.

Our event-related fMRI study uses a factorial design which is the most appropriate to address this issue because it allows a direct comparison along the two critical dimensions on which we want to compare faces and bodies, namely the dimension *stimulus category* (faces/bodies) and the dimension *emotion* (fearful, happy and neutral stimuli) (Friston & Henson, 2006).

METHODS

Participants

The group consisted of 17 right-handed healthy male volunteers (mean \pm standard deviation: 23.0 ± 2.4 years). All participants had normal or correct-to-normal vision and declared having no history of neurological or psychiatric disorders. The study was in accordance with the Declaration of Helsinki and all participants provided informed consent according to the guidelines of the local ethics committee (CMO region Arnhem-Nijmegen, The Netherlands). Participants were paid 10 euros (14 US dollars). Imaging data of three additional participants were discarded from the analysis, because one participant fell asleep and scans of two other participants showed considerable movement artifacts.

Materials

Stimuli consisted of black-and-white pictures of faces and of bodies with the faces covered by a gray mask. For each category fearful, happy, and neutral expressions were used. Face pictures were selected from the Karolinska Directed Emotional Face (KDEF) database (Lundqvist, Flykt, & Öhman, 1998). Body pictures were taken from our own database.

We briefly recall the construction of the body stimuli. A group of 38 male and 46 female amateurs was recruited. Before the photography session, they were instructed with a standardized procedure and received a payment. As part of the instructions, the actors were familiarized with a typical scenario corresponding to each emotion. For example, the fearful scenario was an encounter with a large dangerous dog and the happy scenario was an encounter with a dear friend. Other expressions, such as angry, sad, disgusted and neutral (without performing an action), were also obtained for use in the validation procedure. The neutral postures consisted of six instrumental actions (pouring water into a glass, drinking from a glass, combing one's hair, making a telephone call, putting on trousers, opening a door), of which the instrumental action 'pouring water into a glass' was used in the current fMRI experiment. For the validation a total of 940 face stimuli (consisting of all the basic emotions and the neutral expressions of the KDEF set) and

869 body stimuli (consisting of the emotions mentioned and instrumental actions) were included, which used a total of 120 participants.

Face and body stimuli were presented for 4 s with an inter-stimulus interval of 7 s. Participants were instructed to categorize the emotion displayed by circling on an answer sheet one of seven (face stimuli) or six (emotional body stimuli) response alternatives, or were instructed to categorize the instrumental action displayed by choosing out of six response alternatives. Stimuli that were recognized above 75% were candidates for inclusion in the stimulus set of the fMRI experiment.

A total of 18 face and 18 body images were used in the present study. Each of the expression categories, i.e., fearful, happy, and neutral, comprised different identities, i.e., three males and three females. Faces were fitted inside a gray oval shape, which masked all information to the faces. Body stimuli were cut out, removing all background. The faces of the body pictures were covered with a gray mask that makes the internal facial features invisible. Additionally, a scrambled version of each neutral image was created using a phase-scrambling procedure (Ganis & Kutas, 2003; Malach et al., 1995). All stimuli, including the scrambled images, were resized to 300 pixels in height and presented on a gray background. See Figure 1 for stimulus examples.

Task

Participants of the event-related fMRI experiment were instructed to categorize the emotion

irrespective of whether the stimulus was a face or a body. A trial consisted of a fixation cross (200 ms), followed by a stimulus (500 ms), by a gray screen (1750 ms) and an answer screen (1400 ms) which prompted the participants to respond by pressing one of the three buttons corresponding to the different emotions. Button–emotion pairings varied randomly per trial. To prevent differences in eye-movements between the face and body conditions, a fixation cross was presented throughout the trial in the same position, and the presentation duration of the stimulus was kept to a minimum. The scrambled pictures were presented with strictly the same unfolding in time as the other experimental trials. However, subjects had no judgment to perform during those trials; they just had to select one of the three buttons according to the instruction given on the answer screen. The stimulus set of 48 different images (six faces \times three expressions, six bodies \times three expressions, six neutral scrambled faces, six neutral scrambled bodies) was presented six times, resulting in 288 trials. Null-events were included in our design to establish a better implicit baseline (see Friston, Zarahn, Josephs, Henson, & Dale, 1999), improving statistical power to detect effects of interest. Additionally, 96 null-events consisting of a gray screen lasting the whole trial were included. During the null-event trials participants had to fixate the screen without performing any task. All trials, including the null-event trials, were pseudo-randomly presented during one run. The pseudorandomization ordering for the conditions and the button–emotion pairing ordering were different for each subject. The experiment was preceded by a short practice

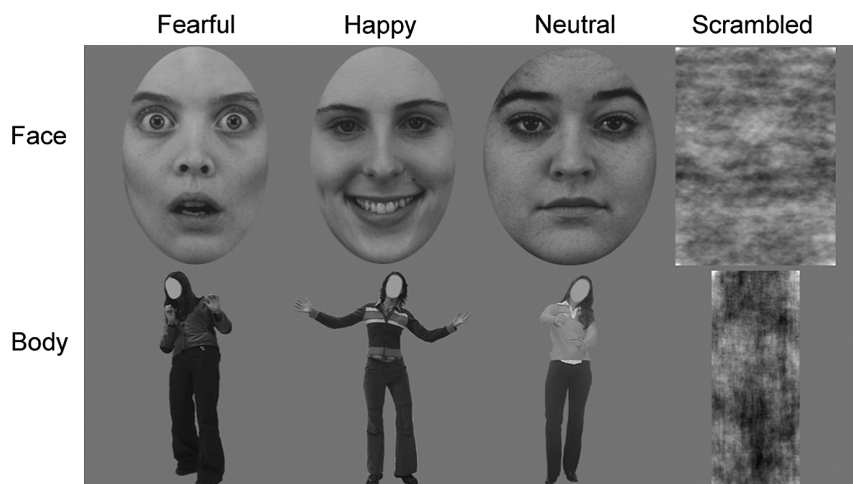


Figure 1. Examples of stimuli used in the experiment showing fearful, happy, neutral and scrambled faces and bodies.

session using different face (Ekman & Friesen, 1976) and body stimuli.

Procedure

Participants lay supine in the scanner with head movements minimized by an adjustable padded head-holder. The stimuli were projected onto a mirror above the participant's head. Responses were recorded via an MR-compatible keypad (MRI Devices, Waukesha, WI), positioned on the right side of the participant's abdomen. A PC running Presentation 9.70 (Neurobehavioral Systems, San Francisco, CA) controlled stimulus presentation and response collection.

fMRI data acquisition

Images were acquired using a 1.5 Tesla Sonata scanner (Siemens, Erlangen, Germany). Blood oxygenation level dependent (BOLD) sensitive functional images were acquired using a single-shot gradient echo-planar imaging (EPI) sequence (repetition time (TR) = 3790 ms; echo time (TE) = 40 ms; 43 transversal slices; ascending acquisition; 2.5 mm slice thickness, with 0.25 mm gap; flip angle (FP) = 90°; field of view (FOV) = 32 cm; matrix size 96 × 64 mm). An automatic shimming procedure was performed before each scanning session. A total of 403 functional volumes were collected for each participant. Following the experimental session, structural images were acquired using an MP-RAGE sequence (TR = 2250 ms; TE = 3.93 ms; inversion time (TI) = 850 ms; voxel size 1 × 1 × 1 mm).

Behavioral data analyses

Behavioral data (reaction times and accuracy) were analyzed using a 2 × 3 repeated-measures analysis of variance (ANOVA) with the main factors Category (i.e., face and body) and Emotion (i.e., fearful, happy, and neutral). When no main effect was observed, conditions were collapsed over the specific factor. Post-hoc one-tailed pair-wise *t* tests were performed to further specify the main effects and interactions.

fMRI data analysis

Imaging data were analyzed using SPM2 (Statistical Parametric Mapping, www.fil.ion.ucl.ac.uk/spm). The first five volumes of each functional run were discarded to allow for T1 equilibration. The remaining 398 functional images were reoriented, slice-time corrected to the middle slice and spatially realigned to the first volume. The images were normalized to the standard MNI (Montreal Neurological Institute) template and subsampled at an isotropic voxel size of 2 mm. The normalized images were smoothed with an isotropic 6 mm full-width-half-maximum (FWHM) Gaussian kernel.

A random effects analysis was performed. The BOLD response to the stimulus onset for each event-type was convolved with the canonical hemodynamic response function of 3.65 s (0.96 TR). For each subject's session, six covariates were included in order to capture residual movement-related artifacts (the three rigid-body translations and the three 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.

At the first level, the following six separate *t*-test contrasts, each representing a separate condition, i.e., fearful (F_FE), happy (F_HA), and neutral (F_NE) face conditions and fearful (B_FE), happy (B_HA), and neutral (B_NE) body conditions, were modeled. The null events were modeled implicitly.

For the second-level analysis, a within-subjects ANOVA was implemented in SPM2 (see Henson & Penny, 2005) using the six separate *t*-test contrasts of interest. A non-sphericity correction was applied to account for variance differences between conditions and subjects. A 2 × 3 ANOVA consisting of the factors Category (i.e., face and body) and Emotion (i.e., fearful, happy, and neutral) was used to calculate the main effect of Category, i.e., Face vs. Body and Body vs. Face. For the main effect of Emotion, we constructed different 2 × 2 ANOVAs consisting of the factors Category (i.e., face and body) and one of the three combinations of the levels of the factor Emotion (fearful-neutral, fearful-happy and happy-neutral). These 2 × 2 ANOVAs were used to calculate the interactions between factors Category and Emotion.

TABLE 1
Overview of calculated contrasts

Contrasts		<i>Masked inclusively by</i>		
<i>Main effects</i>				
Category				
1	Face	Face	> Body	= (F_FE + F_HA + F_NE) - (B_FE + B_HA + B_NE)
2	Body	Body	> Face	= (B_FE + B_HA + B_NE) - (F_FE + F_HA + F_NE)
Emotion				
3	Fearful vs. Neutral	Fearful	> Neutral	= (F_FE + B_FE) - (F_NE + B_NE)
4	Happy vs. Neutral	Happy	> Neutral	= (F_HA + B_HA) - (F_NE + B_NE)
5	Fearful vs. Happy	Fearful	> Happy	= (F_FE + B_FE) - (F_HA + B_HA)
6	Happy vs. Fearful	Happy	> Fearful	= (F_HA + B_HA) - (F_FE + B_FE)
<i>Interaction effects</i>				
7	Fearful face			= (F_FE - F_NE) - (B_FE - B_NE) (F_FE - F_NE)
8	Happy face			= (F_HA - F_NE) - (B_HA - B_NE) (F_HA - F_NE)
9	Fearful body			= (B_FE - B_NE) - (F_FE - F_NE) (B_FE - B_NE)
10	Happy body			= (B_HA - B_NE) - (F_HA - F_NE) (B_HA - B_NE)

Note: F = face; B = body; FE = fearful; HA = happy; NE = neutral.

Each interaction was masked (inclusively) with its simple effect consisting of the comparison of the emotion with its neutral counterpart, i.e., fearful face vs. neutral face for the fearful face specific interaction, happy face vs. neutral face for the happy face specific interaction, fearful body vs. neutral body for the fearful face specific interaction, happy body vs. neutral body for the happy body specific interaction, at $p < .001$ in order to reveal only the significant voxels specific to the perception of respectively fear and happiness in facial and bodily expressions.

A threshold of $p < .001$ (uncorrected for multiple comparisons) was used and clusters of activation with a minimum of 10 contiguous voxels were reported. The resulting 10 contrasts are depicted in Table 1.

Anatomical labeling

Activation patterns of each condition were rendered on the standard MNI brain, i.e., Colin27 (Holmes et al., 1998) in the anatomy toolbox (www.fz-juelich.de/ime/spm_anatomy_toolbox and see Eickhoff et al. (2005) for a description). The atlas of Duvernoy (1999) was used for the macroscopical labeling of the activation clusters. The anatomy toolbox was used for providing cytoarchitectonic labels to the clusters. If the majority of the voxels of the cluster fell within a certain brain region, the corresponding label was applied on the macroscopic and if available on the cytoarchitectonic level. In case a cytoarchi-

tectonic label was applied, the percentage of voxels to which that specific label really applied was given (see caption to Table 2).

RESULTS

Behavioral results

Accuracy of recognizing facial and bodily expressions was very high (fearful face: 95%, happy face: 94%, neutral face: 94%, fearful body: 91%, happy body: 88%, neutral body: 94%). The 2×3 ANOVA for accuracy with the factor Category (face and body) and the factor Emotion (fearful, happy, and neutral) showed a main effect for Category, $F(1, 16) = 6.175, p = .024$. There was no significant main effect for Emotion, $F(2, 15) = 2.363, p = .128$, and no significant interaction between the two categories, $F(2, 15) = 2.810, p = .092$. A 2×3 ANOVA for reaction time (means for fearful face: 683 ms; happy face: 611 ms; neutral face: 667 ms; fearful body: 686 ms; happy body: 629 ms; neutral body: 666 ms) with the factor Category (face and body) and the factor Emotion (fearful, happy, and neutral) showed a main effect for Emotion, $F(2, 15) = 14.546, p = .001$, while a main effect for Category, $F(1, 16) = 0.818, p = .379$, and an interaction between the two categories, $F(2, 15) = 0.981, p = .398$, was not significant. As the factor Emotion consisted of three levels, pair-wise comparisons between the three emotions were performed, with the factor Category collapsed. Participants reacted faster to happy expressions

TABLE 2
Significant activation foci for each contrast

Brain regions			MNI coordinates			Z-value main effects						Interactions			
Macroscopically defined regions ¹	Cytoarchitectonically defined regions	Vox% AT	X	Y	Z	F > B	B > F	FE > NE	HA > NE	FE > HA	HA > FE	F FE	F HA	B FE	B HA
<i>Visual areas</i>															
Fusiform gyrus			L	-44	-52	-18		4.57	4.04		3.85				
			R	44	-48	-18		5.15	5.10		3.98				4.69
			R	42	-62	-12				3.63		3.91			
Inferior occipital gyrus			R	52	-74	-10			3.87		4.13				
	Area 18 ⁴	44.2	L	-34	-90	-14					4.05				
Middle temporal/ Middle occipital gyrus	Area 18 ⁴	57.2	R	22	-90	-18					3.99				
			L	-50	-74	4		6.45†							
Superior temporal sulcus, anterior part			R	54	-66	6		7.40‡							
			R	54	2	-16					3.75				
Superior temporal sulcus, posterior part			R	50	12	-28			4.38					5.09	
			L	-52	-60	24									
Superior occipital gyrus Calcarine sulcus			L	-46	-60	10		4.84†							
			R	50	-44	6			3.95		3.93				
			R	44	-58	10									
			R	36	-84	28			4.72‡						
	Area 17 ⁴	86.4	L	-12	-102	6	3.58								
Lingual gyrus	Area 17 ⁴	97.4	L	-12	-80	6					3.70				
	Area 17 ⁴	30.0	R	8	-98	-6	4.24								
	Area 17 ⁴	57.5	R	12	-70	6					3.66				
Occipital pole	Area 17 ⁴	100.0	R	8	-84	0								3.98	
	Area 17 ⁴	59.4	R	24	-104	-4					4.42				
<i>Subcortical areas/Brain stem</i>															
Amygdala	Amygdala ⁵	79.9	L	-20	-8	-14			4.08		4.19				
	Amygdala ⁵	97.1	R	24	-10	-10			3.71						
Superior colliculus			L/R	0	-32	-4					3.74				
Hypothalamus ²			R	10	-4	-6									3.61
Periaqueductal gray ³			L	-4	-24	-18							4.10		4.49
<i>Sensorimotor regions</i>															
Precentral gyrus	Lateral premotor cortex ⁶	48.9	R	50	4	38				3.93		4.84			
	Lateral premotor cortex ⁶	54.5	R	20	-14	54				3.80		3.92			

TABLE 2 (Continued)

Brain regions			MNI coordinates			Z-value main effects						Interactions					
Macroscopically defined regions ¹	Cytoarchitecturally defined regions	Vox% AT		X	Y	Z	F > B	B > F	FE > NE	HA > NE	FE > HA	HA > FE	F FE	F HA	B FE	B HA	
Central sulcus	M1 ⁷	59.6*	R	32	-32	58				3.57*							
	M1 ⁷	51.3	R	40	-26	56						4.15					
	M1/S1 ^{7,8,9,10}	64.9	L	-40	-22	54						3.51					
	SI ^{8,9,10}	71.9	R	46	-18	52						4.45					
Postcentral gyrus	SI ^{8,9,10}	92.7	L	-52	-14	50								4.60			
	SI ^{8,9,10}	97.8	L	-28	-44	56											
	SI ^{8,9,10}	97.8	R	56	-24	46											
	SI ^{8,9,10}	39.9*	R	22	-32	56				4.01*							
	SI ^{8,9,10}	97.1	R	20	-46	64				4.10							
Superior frontal sulcus	Lateral premotor cortex ⁶	82.8	L	-20	-18	56				3.49							
Superior frontal gyrus, medial part	Pre-SMA ^{6,11}	65.3	L/R	-2	14	56				3.47							
Paracentral lobule	SMA ^{6,11}	65.5	L/R	0	-8	74				3.50							
	SMA ^{6,11}	28.8	R	4	-12	76						3.50					
	M1 ⁷	98.3	L	-8	-36	66				3.39							
Caudate nucleus, head			R	8	4	6									3.96		4.32
Putamen			L	-20	16	2											3.88
Cerebellum			R	10	-84	-30								4.06	4.35		
			R	40	-80	-36	4.15										
			R	16	-56	-30				3.66							
			R	10	-58	-6						3.34					
<i>Other frontal regions</i>																	
Inferior frontal gyrus, pars triangularis	Area 45 ¹²	75.6	L	-56	22	8				4.33							
	Area 45 ¹²	51.6	L	-48	26	24											4.68
	Area 45 ¹²	100.0	R	48	22	6											3.48
	Area 45 ¹²	51.1	R	54	24	26											4.64
Inferior frontal gyrus, pars orbitalis			L	-50	18	-2											3.54
Superior frontal sulcus			L	-20	14	58				3.74							
			L	-22	26	56						3.74					
			R	26	8	48						4.40					
Inferior frontal sulcus			L	-40	38	12									4.35		4.41
			L	-38	22	26									3.67		
			L	-32	4	30											4.58
			R	46	12	30											3.79

TABLE 2 (Continued)

Brain regions			MNI coordinates			Z-value main effects						Interactions			
Macroscopically defined regions ¹	Cytoarchitectonically defined regions	Vox% AT	X	Y	Z	F > B	B > F	FE > NE	HA > NE	FE > HA	HA > FE	F > FE	F > HA	B > FE	B > HA
Middle frontal gyrus		L	-36	56	14					3.72					
Frontal operculum		L	-38	10	22					3.64					
Superior frontal gyrus, medial part		L/R	-4	22	48				3.78						4.44
Superior frontal gyrus		R	10	44	42										4.22
		L	-12	32	58						4.41				
		L	-20	14	62						3.79				
Postcentral sulcus		L	-18	-50	50						4.01				
Olfactory sulcus		L	-16	18	-16				4.06						
Anterior cingulate gyrus		R	4	38	-2	3.68									
Cingulate sulcus		L	-10	-24	42								3.74		
<i>Parietal regions</i>															
Superior parietal lobule		L	-18	-50	50				4.18						
Parieto-occipital sulcus		L	-8	-78	48		3.61								
		R	12	-80	46		3.98								
		R	16	-68	24		3.66								
Intraparietal sulcus		R	32	-66	52		3.63		3.82						
	Area hIP1 ¹³	L	-42	-54	38						3.55				
Precuneus		L	-10	-62	46						4.00				
		L/R	0	-54	64					3.93					
Subparietal sulcus		R	4	-46	40						3.98				
<i>Other regions</i>															
Insula		L	-32	-20	24				4.24						
		L	-38	8	0				3.58						
Insula/Inferior frontal gyrus, pars orbitalis		L	-38	20	-6			3.75	3.67						
Parahippocampal gyrus	Subicular complex ⁵	33.0	L	-12	-42	-4			4.06						
	Subicular complex ⁵	93.8	R	22	-28	-12					4.17				
Superior temporal gyrus		L	-56	4	2						3.89				

Notes: Brain regions are labeled according to criteria of: (1) Duvernoy (1999) (except where noted); (2) Mai, Assheuer, & Paxinos (2003); (3) Nieuwenhuys, Voogd, & van Huijzen (1988); (4) Amunts, Malikovic, Mohlberg, Schormann, & Zilles (2000); Amunts et al. (2005); Geyer (2004); (7) Geyer et al. (1996); (8) Geyer, Schleicher, & Zilles (1999); (9) Geyer, Schormann, Mohlberg, & Zilles (2000); (10) Grefkes, Geyer, Schormann, Roland, & Zilles (2001); (11) Picard & Strick (1996); (12) Amunts et al. (1999); (13) Choi et al. (2006). Area hIP1 = human intraparietal area 1; AT = Anatomy Toolbox; B = body; F = face; FE = fearful; HA = happy; L = left; M1 = primary motor cortex; MNI = Montreal Neurological Institute; NE = neutral; pre-SMA = presupplementary motor area; R = right; SI = primary somatosensory cortex; SMA = supplementary motor area; Vox = voxels. Z-values of activations that are appended † or ‡ or • consist of multiple local maxima that fall in different anatomically defined regions. If Z-values are appended with the same symbol, i.e., † or ‡ or •, they belong to the same cluster. * = The reported activation of the central sulcus/M1 and postcentral gyrus/SI belong to the same cluster. Percentages for the cytoarchitectonically defined regions are percentages of the whole cluster.

than to neutral, $t(16) = -5.180$, $p < .001$, or fearful expressions, $t(16) = 4.895$, $p < .001$. The difference between the fearful and neutral expressions was not significant, $t(16) = 1.750$; $p = .099$.

fMRI results

Table 2 summarizes the results of the 2×3 ANOVA and the different 2×2 ANOVAs. We present first the main effects of the ANOVAs of Category (i.e., Face > Body and Body > Face) and Emotion (i.e., Fearful > Neutral, Happy > Neutral, Fearful > Happy, and Happy > Fearful) followed by the specific interactions (i.e., Fearful Face, Happy Face, Fearful Body, and Happy Body).

Main effects

The *face vs. body* contrast yielded activations in the calcarine sulcus, anterior cingulate gyrus, and cerebellum.

The *body vs. face* contrast yielded more activity in the left and right fusiform gyrus for the presentation of bodies than for faces (see Figure 2). A large blob covering the middle occipital and middle temporal gyrus and the posterior part of the superior temporal sulcus was seen in the body vs. face contrast (see Figure 3). The part covering the middle temporal and middle occipital gyrus included area V5/MT (as seen in the anatomy toolbox) and the extrastriate body area (as the local maximum of the Downing et al. (2001) study falls within the extent of our blob). In what follows

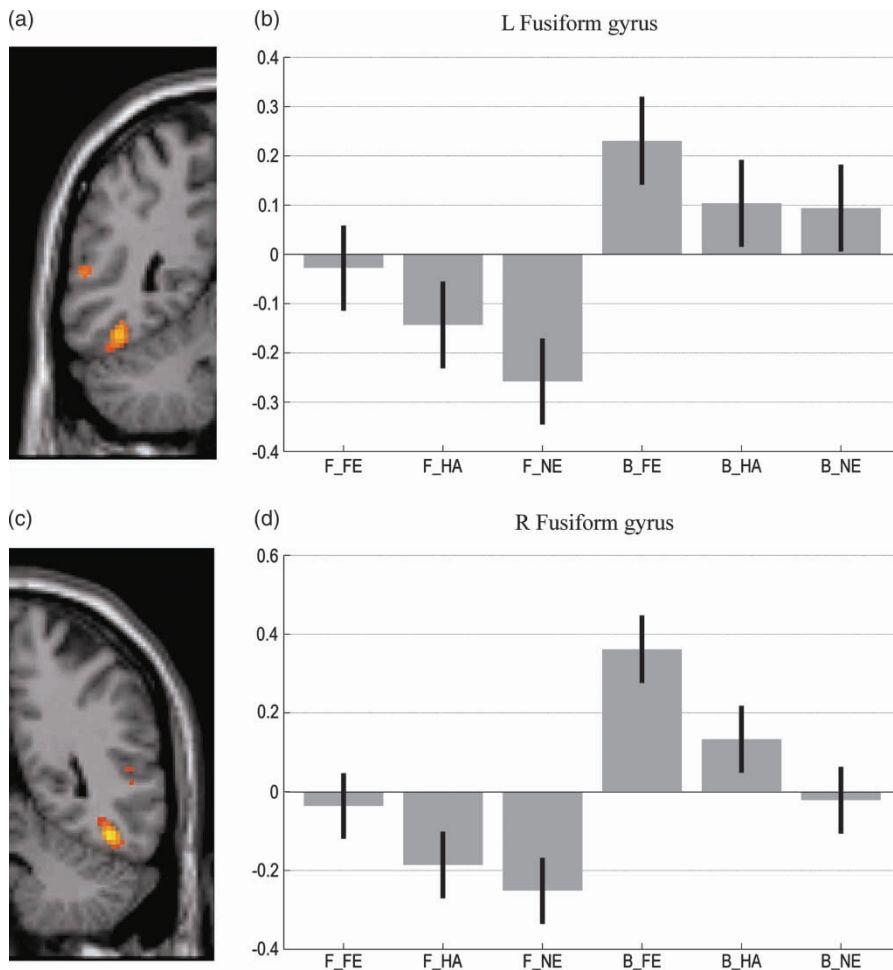


Figure 2. Body vs. face contrast for the left and right fusiform gyrus. (a) Group ($N = 17$) average activation of the left fusiform gyrus on a coronal section ($y = -52$) of the MNI brain. (b) Mean value of the parameter estimates (arbitrary units, mean centered) for the maxima of the left fusiform gyrus ($x, y, z = -44, -52, -18$) for fearful face (F_FE), happy face (F_HA), neutral face (F_NE), fearful body (B_FE), happy body (B_HA), and neutral body (B_NE). (c) Group ($N = 17$) average for the right fusiform gyrus on a coronal section ($y = -48$) of the MNI brain. (d) Mean value of the parameter estimates (arbitrary units, mean centered) for the maxima of the right fusiform gyrus ($x, y, z = 44, -48, -18$) for the same six conditions.

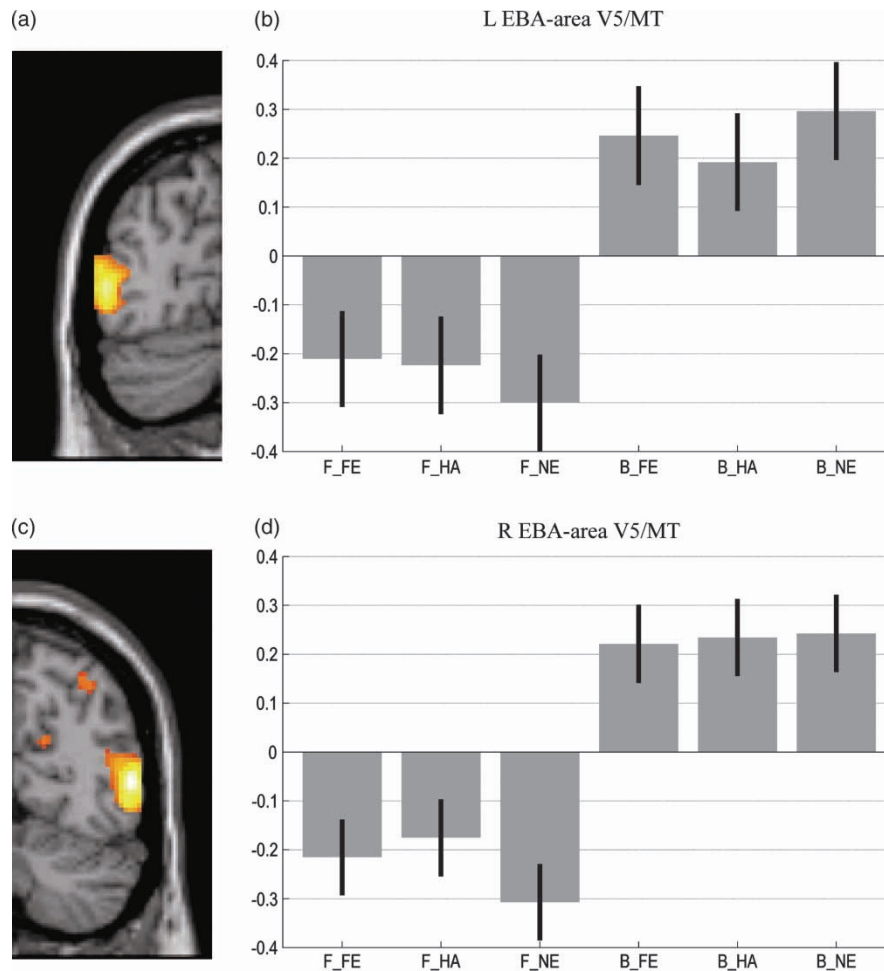


Figure 3. Body vs. face contrast for the left and right extrastriate body area – area V5/MT (EBA-area V5/MT). (a) Group ($N=17$) average activation of the left extrastriate body area–area V5/MT on a coronal section ($y = -74$) of the MNI brain. (b) Mean value of the parameter estimates (arbitrary units, mean centered) for the maxima of the left extrastriate body area–area V5/MT ($x, y, z = -50, -74, 4$) for fearful face (F_FE), happy face (F_HA), neutral face (F_NE), fearful body (B_FE), happy body (B_HA), and neutral body (B_NE). (c) Group ($N=17$) average for the right extrastriate body area–area V5/MT on a coronal section ($y = -66$) of the MNI brain. (d) Mean value of the parameter estimates (arbitrary units, mean centered) for the maxima of the right extrastriate body area–area V5/MT ($x, y, z = 54, -66, 6$) for the same six conditions.

we refer to this as ‘extrastriate body area–area V5/MT’. Additionally we found some activity in the parietal lobe (i.e., intraparietal sulcus and parieto-occipital sulcus).

The *fearful vs. neutral* contrast showed bilateral activation in the amygdala (see Figure 4). The left and right fusiform gyrus and the right inferior occipital gyrus were more activated for the presentation of fearful than for neutral expressions. Other regions included the right superior temporal sulcus (see Figure 5), a region overlapping the pars orbitalis of the inferior frontal gyrus and the insula, and the pars triangularis of the inferior frontal gyrus, including Brodmann area 45.

The *happy vs. neutral* contrast shows more activity in the right fusiform gyrus for happy

expressions than for neutral ones. The local maximum of this contrast was somewhat more posterior than the one displayed in Figure 2. The happy expressions activated more the parietal lobe (i.e., superior parietal lobule and intraparietal sulcus), some sensorimotor areas (i.e., primary motor cortex, premotor cortex, and primary somatosensory cortex), the olfactory sulcus and the insula.

The *fearful vs. happy* contrast yielded activation in left amygdala, left and right fusiform gyrus, right inferior occipital gyrus, and right superior temporal sulcus.

The *happy vs. fearful* contrast shows also more activity in the right fusiform gyrus for happy than for fearful expressions. In contrast to the fearful expression we observe condition-specific

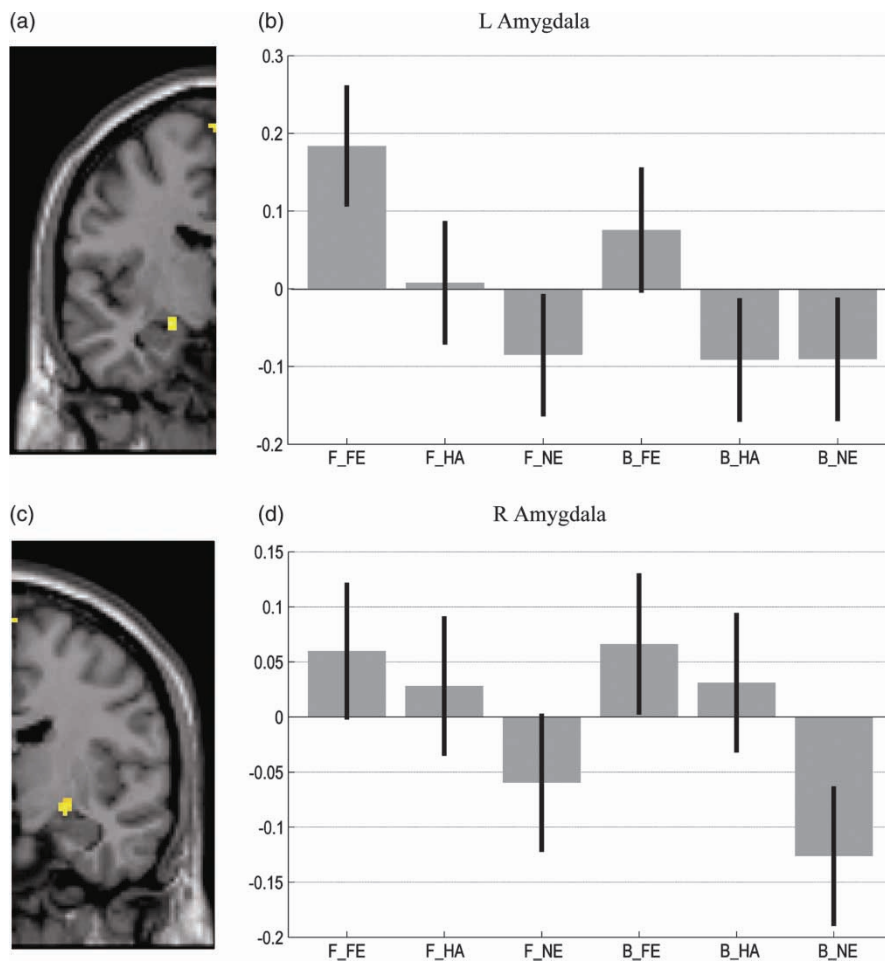


Figure 4. Fearful vs. neutral contrast for the left and right amygdala. (a) Group ($N=17$) average activation of the left amygdala on a coronal section ($y = -8$) of the MNI brain. (b) Mean value of the parameter estimates (arbitrary units, mean centered) for the maxima of the left amygdala ($x, y, z = -20, -8, -14$) for fearful face (F_FE), happy face (F_HA), neutral face (F_NE), fearful body (B_FE), happy body (B_HA), and neutral body (B_NE). (c) Group ($N=17$) average for right amygdala on a coronal section ($y = -10$) of the MNI brain. (d) Mean value of the parameter estimates (arbitrary units, mean centered) for the maxima of the right amygdala ($x, y, z = 24, -10, -10$) for the same six conditions.

activation for the happy expressions in the anterior part of the superior temporal sulcus, the parietal lobe (i.e., precuneus, postcentral sulcus), and some sensorimotor areas (i.e., primary motor cortex, premotor cortex, and primary somatosensory cortex).

Interaction effects

The *Fearful Face* contrast showed that the added effect of the fearful expression was larger for activity in the superior temporal sulcus in reaction to faces than for bodies. In the *Happy Face* contrast the primary somatosensory cortex, the cerebellum and the cingulate sulcus were activated. In the *Fearful Body* contrast the periaqueductal gray, the head of the caudate

nucleus, and the inferior frontal sulcus were shown to be activated. In the *Happy Body* contrast the left fusiform gyrus, the periaqueductal gray, and the hypothalamus emerged as well as the pars triangularis of the inferior frontal gyrus (cytoarchitectonically Brodmann area 45).

DISCUSSION

Our goal was to investigate at the level of the whole brain what neural substrates are common and specific to perceiving neutral or emotional faces and bodies.

Our major findings are as follows. First, our results clearly show the important role of the amygdala and the fusiform gyrus in recognizing

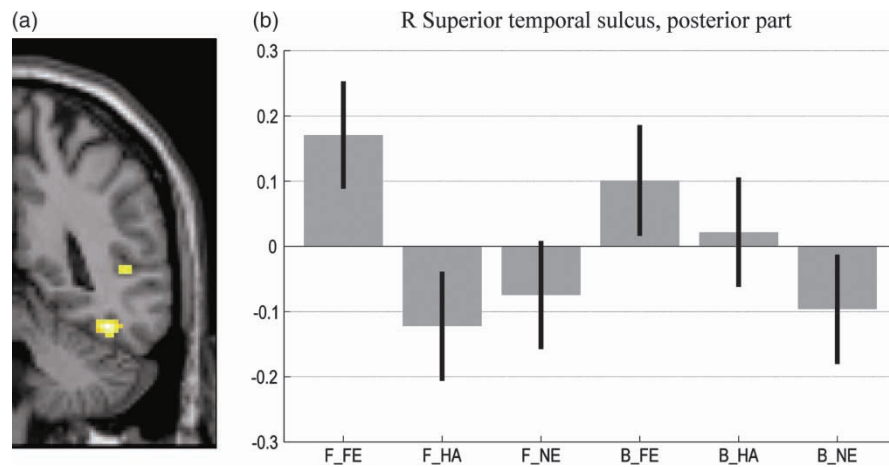


Figure 5. Fearful vs. neutral contrast for the posterior part of the right superior temporal sulcus. (a) Group ($N=17$) average activation of the posterior part of the right superior temporal sulcus on a coronal section ($y = -44$) of the MNI brain. (b) Mean value of the parameter estimates (arbitrary units, mean centered) for the maxima of the posterior part of the right superior temporal sulcus ($x, y, z = 50, -44, 6$) for fearful face (F_FE), happy face (F_HA), neutral face (F_NE), fearful body (B_FE), happy body (B_HA), and neutral body (B_NE).

emotional signals whether in the face or in the whole body. This is demonstrated by our main effect of emotion. Second, the extrastriate body area—area V5/MT in the middle temporal and occipital gyrus is specifically involved in processing bodies but is not sensitive to the emotion displayed. Third, a differential pattern of activations is observed for facial and bodily expressions of fear and happiness. This is evident in the most prominent areas known from the literature but also in the extended network devoted to emotion perception. Finally, we found that other important areas besides face and body areas known for their involvement in processing social information are sensitive to bodily expressions.

Emotion representation of faces and bodies in the fusiform gyrus

Our results add important new information concerning the similarity between face- and body-induced activity in the fusiform gyrus by the expression. We observed more activity in the left and the right fusiform gyrus when participants perceived bodies as compared to faces and also specifically when participants perceived fearful compared to neutral or happy expressions. The fact that this region is not revealed by the interaction between the fearful vs. neutral expression and face category or between fearful vs. neutral expression and body category suggests that the presence of a fearful emotional expres-

sion has the same additive effect on the fusiform gyrus activity for faces and bodies. We thus conclude that even if there is more activity in the fusiform gyrus when body stimuli are presented compared to faces, the modulation induced by the fearful condition is the same for faces and for bodies. For the other emotion, the effect obtains whether a face or body expresses happiness. There is no difference for the right fusiform gyrus, but the increase in activation for the left fusiform gyrus is only seen for the presentation of the happy body and not for the presentation of the happy face.

We did not find any evidence for segregation between regions in the fusiform gyrus responsive either for faces or bodies as argued for by Peelen and Downing (2005) and Schwarzlose et al. (2005). There may be several reasons for this. One is that in contrast to Schwarzlose et al. (2005) we did not use high-resolution scanning. Next, the data were analyzed on group level and smoothing was applied on the data of each subject, a procedure that may obscure small effects. Third, unlike what was done here, the Peelen and Downing study did not contrast directly faces and bodies but instead faces and bodies were each separately contrasted to tools. The study of Schwarzlose shows that the differences between faces and bodies for the fusiform face area with normal-resolution scanning are rather marginal and this is also the case for the difference between these two categories for the fusiform body area, while difference between faces and bodies in

contrast to cars and assorted objects is larger. Therefore, contrasting faces to tools and bodies to tools may more easily yield significant voxels for faces and bodies respectively than a direct comparison between faces and bodies as done in the current study. However, the use of multivoxel pattern analysis (Downing, Wiggett, & Peelen, 2007; Peelen & Downing, 2007a, 2007b; Peelen et al., 2006) could have identified overlapping regions of the fusiform gyrus separately selective for faces and bodies.

Amygdala activity is observed when we compare the fearful facial and bodily expressions to the neutral ones but not when we compare happy facial and bodily expressions to their neutral counterparts. This is consistent with amygdala lesion studies showing that affected patients are most profoundly impaired in the recognition of fearful facial expressions (Adolphs et al., 1994, 1999; Anderson & Phelps, 1998; Hamann et al., 1996). Previous neuroimaging studies showed amygdala involvement in perceiving fearful facial (Breiter et al., 1996; Morris et al., 1998; Phillips et al., 1997; Whalen et al., 1998) and bodily expressions (de Gelder et al., 2004; Hadjikhani & de Gelder, 2003) with no amygdala activation for happy facial (e.g., Iidaka et al., 2001) or bodily (de Gelder et al., 2004) expressions. But our study was not designed as a systematic comparison of all basic emotions and our conclusions are so far restricted to the emotion investigated here. For example, our findings are not incompatible with the role of the amygdala as a relevance detector (Sander, Grafman, & Zalla, 2003). In line with this, an increasing number of studies challenge this fear selectivity (Breiter et al., 1996; Fitzgerald, Angstadt, Jelsone, Nathan, & Phan, 2006; Pessoa, McKenna, Gutierrez, & Ungerleider, 2002; Pichon et al., in press; van der Gaag, Minderaa, & Keysers, 2007; Williams, Morris, McGlone, Abbott, & Mattingley, 2004; Winston, O'Doherty, & Dolan, 2003).

Our results are consistent with the study by Sprengelmeyer et al. (1999) using faces and bodies but not with the conclusions from Adolphs and Tranel (2003). The first study showed that a patient with bilateral amygdala damage was impaired in recognizing not only fearful facial expressions but also fearful bodily expressions, while his performance on recognizing happy bodily expressions was at ceiling. In contrast to the study of Sprengelmeyer et al. (1999), the results here, and previous studies (de Gelder et al., 2004; Grèzes et al., 2007; Grosbras &

Paus, 2006), Adolphs and Tranel concluded that the presence of a facial expression is a *conditio sine qua non* for amygdala involvement because observing bodies with blanked-out facial expressions did not hamper performance in patients with amygdala lesions, while performance dropped for control participants. It is worth noting, though, that their stimuli were complex and showed an interaction within a pair of actors, one of which showed aggression to the other.

Quite similarly, a recent study by Atkinson, Heberlein, and Adolphs (2007) also questions the involvement of the amygdala in judging fear from static and dynamic body postures. This study elegantly shows that despite a selective lesion of the amygdala, due to Urbach-Wiethe disease, two patients are quit able to categorize correctly static and dynamic bodily expressions of fear. However, this does not rule out the involvement of the amygdala. The amygdala could still be activated in our experiment or in life in general, during the early evaluation of fearful body language. The patients with the Urbach-Wiethe disease had in the experiment an unlimited amount of time during the categorization of the static and dynamic body postures, enabling them to rely on knowledge and cognitive processes to judge the emotion conveyed by the bodily posture.

In addition to the activity in the amygdala, another subcortical structure, i.e., the superior colliculus was activated more by the fearful than by the happy expressions. Other studies (de Gelder et al., 2004; Morris, deBonis, & Dolan, 2002) have already pointed to the reactivity of the superior colliculus to fearful expressions.

The body vs. face contrast showed a large bilateral activation in a region encompassing the middle temporal gyrus and the middle occipital gyrus. These blobs overlap with area V5/MT (Allman & Kaas, 1971), a region in the brain sensitive for the perception of motion. In human subjects the normal procedure to localize area V5/MT is to use a functional motion localizer (e.g., Tootell et al., 1995). By projecting our data in the anatomy toolbox (Eickhoff et al., 2005) we were able to locate the activity in the middle occipital gyrus/middle temporal gyrus relative to area V5/MT (Malikovic et al., 2007). The spatial extent of our activation was much larger than the region comprising area V5/MT and also encompassed the extrastriate body area (Downing et al., 2001). The study of Spiridon et al. (2006) showed that the area V5/MT is located intermediately

between an anterior and a posterior part of the extrastriate body area, making it difficult to determine whether the extrastriate body area or the area V5/MT or both are primarily active within an activation cluster. The locations of the additional local maxima are in agreement with the location of the extrastriate body area in other studies (e.g., Downing et al., 2001; Spiridon et al., 2006). This issue becomes more complicated when taking into account the results from the study of Kourtzi and Kanwisher (2000), which showed that area V5/MT was activated by body stimuli with implied movement. The implied movement component possibly present in the bodily expression stimuli used in the current study could be responsible for the activations in area V5/MT. In the current study and in line with our previous one (de Gelder et al., 2004) no differences in activation in the extrastriate body area–area V5/MT was found between the three bodily expressions (i.e., fearful, happy and neutral), indicating that this complex is not sensitive to emotional modulation.

Specific and common representation in the emotion network

As already known from previous studies, other important areas besides the amygdala and the fusiform gyrus are involved in processing facial and bodily expressions. With the present systematic comparison we observe a main effect of fearful expression in the right inferior occipital gyrus, a location comparable to that of the occipital face area (Allison et al., 2000; Puce et al., 1996). This finding is consistent with other studies using movement (Grosbras & Paus, 2006), emotional facial (Ishai, Pessoa, Bickle, & Ungerleider, 2004; Schmidt, Boesiger, & Ishai, 2005), and bodily expressions (Grèzes et al., 2007). They reported also larger activity for the emotional compared to the neutral expressions.

Several parts of the superior temporal sulcus were activated by the presentation of fearful faces and bodies as shown by a main effect of fearful vs. neutral expression in the anterior and posterior part of the right superior temporal sulcus as well as a specific fearful face effect for the posterior part of the left superior temporal sulcus. Additionally a more anterior focus in the anterior part of the superior temporal sulcus showed more activation for the happy than the fearful expressions. The posterior part of the left and right

superior temporal sulcus showed a main effect for the body category. The location of the activation in the posterior part of the superior temporal sulcus as seen in the body vs. face contrast was not identical to the activations in the posterior part of the superior temporal sulcus elicited by the fearful vs. neutral expression contrast. The first one resided in the horizontal posterior branch of the superior temporal sulcus while the second resided in the ascending posterior branch of the superior temporal sulcus.

Sensitivity of the superior temporal sulcus for faces and bodies conveying an emotion is consistent with earlier single-cell recordings in monkeys that showed the presence of face selective cells in the monkey superior temporal sulcus (e.g., Baylis et al., 1985; Bruce et al., 1981; Mikami et al., 1994) and additional cells responding to body posture (e.g., Hasselmo, Rolls, Baylis, & Nalwa, 1989; Perrett et al., 1989), while other studies demonstrated the sensitivity of the superior temporal sulcus for the emotional expression conveyed by the face (in monkey: Hasselmo, Rolls, & Baylis, 1989; in human: Narumoto, Okada, Sadato, Fukui, & Yonekura, 2001) or by the body (in human: Grèzes et al., 2007). Sensitivity of the superior temporal sulcus for emotional expression may be based on connections between the superior temporal sulcus and the amygdala (Stefanacci & Amaral, 2000).

Another interesting aspect of the present results is that the insula/pars orbitalis of the inferior frontal gyrus seems to be sensitive to both fearful and happy expressions. It has been suggested that the insula is specifically involved in the recognition and/or processing of disgust (Phillips et al., 1997; Sprengelmeyer, Rausch, Eysel, & Przuntek, 1998; Wicker et al., 2003). However the studies of Schienle et al. (2002) and Chua, Krams, Toni, Passingham, and Dolan (1999) show the involvement of the insula in fear processes. More specifically, Gorno-Tempini et al. (2001) and Damasio et al. (2000) reported insula involvement in fear and happiness processes, which is in line with our results.

Besides the amygdala and the superior colliculus, other subcortical structures were involved for the perception of emotional expressions, mainly the hypothalamus specifically for happy bodily expressions and the periaqueductal gray for fearful and happy bodily expressions. Hypothalamus activation has been found earlier in neuroimaging studies involving food intake (de Araujo & Rolls, 2004; Matsuda et al., 1999),

sexual arousal (Ferretti et al., 2005) and listening to pleasant music (Menon & Levitin, 2005), but also in the self-generation of happiness (Damasio et al., 2000). The involvement of the periaqueductal gray seems to be primarily compatible with the reaction to fearful bodies, e.g., motor quiescence or freezing, and flight reaction (e.g., McNaughton & Corr, 2004) but this area may also play a role in positive emotions (Rolls et al., 2003).

Some motor structures, such as the caudate nucleus, were involved in perceiving both fearful and happy bodies. Interestingly, the caudate nucleus is well known for its involvement in motor preparation (Alexander, DeLong, & Strick, 1986; Hikosaka, Sakamoto, & Usui, 1989a, 1989b; Watanabe, Lauwereyns, & Hikosaka, 2003) and is damaged in patients with Huntington's disease (Harris et al., 1996), a disease characterized by motor disorders (Huntington, 1872) as well as emotion deficits (Jacobs, Shuren, & Heilman, 1995).

Area 45 seems to be involved in object-related observation but also in pantomime without objects (Decety et al., 1997). As argued previously (de Gelder et al., 2004), this region might be involved in representation of the action displayed in the emotional bodily expressions. In contrast to that study, we did not observe a difference here (as demonstrated by the specific interactions) between the fearful facial and bodily expressions, but there is a difference between the happy facial and bodily expressions. Furthermore, we did not find extensive activation in premotor, primary motor, and somatosensory cortices in response to fearful bodies or to the fearful expression but mainly to the happy expressions. The study of de Gelder used a passive viewing task, while the present study used an emotion categorization task. Lange et al. (2003) had already showed that difference in tasks, i.e., passive viewing, gender categorization or emotional categorization, can give rise to different activation patterns. Emphasis on explicit recognition and the use of verbal labeling may contribute to reducing activity in these motor areas, which are often associated with reflex-like responses. However, the similarities between our study and the studies of Hadjikhani and de Gelder (2003) and de Gelder et al. (2004), i.e., involvement of the fusiform gyrus and the amygdala in perceiving fearful bodily expressions, still warrant not attributing all our results to task requirements, as these two

studies used passive viewing and our study an emotional categorization task.

The rapidly extending literature on the perception of emotional bodies and its neural basis indicates that the brain processes emotional bodies effortlessly and rapidly. In doing so it relies on mechanisms that involve neural resources known to have a role in perceiving emotional signals from facial expressions. Yet past research may have attributed too much importance to faces or given too little attention to what is unique about facial emotion communication. To better understand what is unique about facial expressions, the comparison with bodies is essential. For example, it makes sense to expect that emotional communication exclusively centered on the face triggers more empathy-related processing. In contrast, when the emotion is exclusively communicated with the body language, more emotion-action structures may be triggered. Furthermore, the context in which the emotional communication takes place may also be quite different depending on whether the focus is on the face or on the body. Naturalistic facial communication takes place between agents that are nearby while bodily communication can easily take place over a larger distance. Different context factors may be associated with the same emotion whether it is expressed by the face or the body. Future studies need to address the question whether the present findings generalize to other emotions such as anger and sadness. Likewise, we do not know at present whether the pattern of results also obtains when dynamic images of emotional expressions in face and body are compared. Additionally, once we have identified the relevant regions, future functional connectivity analyses need to be performed to shed light on the functional connectivity between them.

Manuscript received 18 June 2007
Manuscript accepted 26 November 2007

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