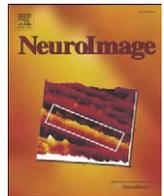




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Similarities and differences in perceiving threat from dynamic faces and bodies. An fMRI study

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ABSTRACT

Neuroscientific research on the perception of emotional signals has mainly focused on how the brain processes threat signals from photographs of facial expressions. Much less is known about body postures or about the processing of dynamic images. We undertook a systematic comparison of the neurofunctional network dedicated to processing facial and bodily expressions. Two functional magnetic resonance imaging (fMRI) experiments investigated whether areas involved in processing social signals are activated differently by threatening signals (fear and anger) from facial or bodily expressions. The amygdala (AMG) was more active for facial than for bodily expressions. Body stimuli triggered higher activation than face stimuli in a number of areas. These were the cuneus, fusiform gyrus (FG), extrastriate body area (EBA), temporoparietal junction (TPJ), superior parietal lobule (SPL), primary somatosensory cortex (SI), as well as the thalamus. Emotion-specific effects were found in TPJ and FG for bodies and faces alike. EBA and superior temporal sulcus (STS) were more activated by threatening bodies.

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Introduction

Perception of bodies and bodily expressions is a relatively novel topic in affective neuroscience, a field dominated so far by investigations of facial expressions. But faces and bodies are equally salient and familiar in daily life and often convey the same information about identity, emotion and gender. Therefore, it seems natural to expect that many of the same research questions arise about both (de Gelder, 2006; de Gelder et al., 2010). On the other hand, differences in the neural basis of body and face processing may be as interesting as the similarities. The goal of our study was to further our understanding of both by systematically comparing facial and bodily expressions of the same emotions.

The neural network underlying face perception is well known and includes the fusiform face area (FFA) (Kanwisher et al., 1997), the occipital face area (OFA) (Gauthier et al., 2000; Puce et al., 1996), the STS and the AMG (Haxby et al., 2000). Recent studies indicate that the neural network underlying whole body perception partly overlaps with the face network (de Gelder, 2006; de Gelder et al., 2010; Peelen and Downing, 2007). But so far, the few direct comparisons have used static images (Meeren et al., 2008; van de Riet et al., 2009). These studies mainly confirm the involvement of AMG, FG, and STS in face and body perception. Furthermore, it remains unclear how activity in these

regions is influenced by dynamic information. Static body pictures may imply motion, but explicit movement information in dynamic stimuli may activate a richer and partly different, broader network.

Recent studies with dynamic stimuli have proven useful for better understanding the respective contribution of action and emotion-related components. A study by Grosbras and Paus (2006) showed that video clips of angry hands trigger activations that largely overlap with those reported for facial expressions in the FG. Increased responses in STS and TPJ have been reported for dynamic threatening body expressions (Grèzes et al., 2007; Pichon et al., 2008, 2009). Whereas TPJ is implicated in higher level social cognitive processing (Decety and Lamm, 2007), STS has been frequently highlighted in biological motion studies (Allison et al., 2000) and shows specific activity for goal-directed actions and configural and kinematic information from body movements (Bonda et al., 1996; Grossman and Blake, 2002; Perrett et al., 1989; Thompson et al., 2005).

There are also some currently unanswered questions about the functional role of body and face selective areas. A body-sensitive area in the extra striate cortex (EBA) was first reported by Downing et al. (2001). Its role in processing dynamic stimuli and affective valence is not yet clear. Urgesi et al. (2007) attribute featural but not configural processing to EBA (see also Taylor et al., 2007; Hodzic et al., 2009). Previous studies using static stimuli failed to find evidence for emotion modulation (de Gelder et al., 2004; Lamm and Decety 2008; van de Riet et al., 2009), but studies of dynamic bodily expressions show that EBA is sensitive to affective information conveyed by the

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body stimulus (Grèzes et al., 2007; Peelen et al., 2007; Pichon et al., 2008). This modulation by emotion may be compatible with EBA as a feature processor, in which case one would need to investigate which specific body part conveys the affective information. Alternatively, EBA does in fact process the configuration of the stimulus. This alternative is consistent with our findings that EBA is differentially sensitive to affective information in the body when videos are used. Originally, Hadjikhani and de Gelder (2003) compared neutral bodies and fear bodily expressions and reported sensitivity for fear bodies in FG. Consistent with this body sensitivity of FG, a later study using neutral bodies, defined a body-sensitive area in the FG labeled the fusiform body area (FBA) (Peelen and Downing, 2005). The role of the EBA and FG in emotional processing has not been fully understood yet, and it is too early to claim that EBA is specifically sensitive for bodily features and less or not sensitive to the configural representation of a body. The use of dynamic emotional stimuli and a direct comparison with facial expressions is likely to provide new insights in this matter.

We used fMRI to measure participants' haemodynamic brain activity while they were watching videos showing fearful, angry or neutral facial or bodily expressions. A major goal was to clarify the sensitivity of AMG, FG, EBA, STS and TPJ for affective valence of whole bodies and of faces. We used a ROI procedure to localize each of these regions. We predicted an increased BOLD response in these areas for facial and bodily expressions of emotion compared to neutral faces and bodies. A second goal was to clarify the emotion-sensitivity of EBA. Since studies that use dynamic stimuli find emotional modulation in this area, we expected to find this area especially active for threatening body expressions.

Methods

Participants

Twenty-eight (14 females, mean age 19.8 years old, range 18–27 years old; 14 males; mean age: 21.6 years old, range 18–32 years old) took part in the experiment. Half of the participants viewed neutral and angry expressions and the other half viewed neutral and fearful expressions. Participants had no neurological or psychiatric history, were right-handed and had normal or corrected-to-normal vision. All gave informed consent. The study was performed in accordance to the *Declaration of Helsinki* and was approved by the local medical ethical committee. Two participants were discarded from analysis, due to task miscomprehension and neurological abnormalities and analyses were done over 26 participants.

Materials

Video recordings were made of 26 actors expressing six different facial and bodily emotions. All actors were dressed in black and filmed against a green background. For the facial videos, actors wore a green shirt, similar as the background color. To coach the actors to achieve a natural expression, pictures of emotional scenes were, with the help of a projector, shown on the wall in front of them and a short emotion inducing story was read out by the experimenter. Additionally, the stimulus set included neutral nonexpressive face and body movements (such as pulling up the nose, twitching/licking lips, coughing, fixing one's hair, or clothes). Recordings used a digital video camera under controlled and standardized lighting conditions in a recording studio. All video clips were computer-edited using Ulead and After Effects, to a uniform length of two seconds (50 frames). The faces of the body videos were masked with Gaussian masks so that only information of the body was perceived.

For each actor and emotion, a few different versions were filmed. These materials were given to five independent raters and they selected the best actors and of these the two best videos per emotion and per actor. The total number of video clips selected was sixty (five male and five female actors, three emotions and two videos each). These materials were then used in a validation study and presented

twice to 20 independent raters. In the validation, participants selected among six emotion labels (anger, fear, surprise, sad, disgust and happy). Angry facial expressions were correctly recognized for 84% (SD 19), fearful facial expressions for 86% (SD 7), neutral facial expressions for 79% (SD 21) angry bodily expressions for 85% (SD 15), fearful body expressions for 83% (SD 16) and neutral body expressions for 80% (SD 20). The participants from the current study also had to label the selected videos after the scanning sessions. All expressions were recognized above 82% correct and there was no difference between anger and fear ($t(24) = .310, ns$).

To check for quantitative differences in movement between the 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 (Grèzes et al., 2007; Peelen et al., 2007). For each frame (50 in total), these absolute 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 were then averaged for each movie. Student's two-tailed *t*-tests were conducted to check whether the amount of movement differed between neutral and threatening movies. Angry and fearful expressions contained equal movement ($M = 30.64, SD 11.99$ vs. $M = 25.41, SD 8.71$) [$t(19) = .776, ns$], but more than neutral expressions ($M = 10.17, SD 6.00$) [$t(19) = 3.78, p \leq .005, d = 2.14$] and [$t(19) = 4.09, p \leq .005, d = 2.04$]. In addition, by using Matlab software, we generated scrambled movies by applying a Fourier-based algorithm onto each movie, a technique that has been used for pictures before (Hoffman et al., 2007). This technique scrambles the phase spectra of each movie's frames and allows to generate video clips served as low-level visual controls and prevents habituation to the stimuli.

Experimental design

The experiment consisted of a total of 176 trials (80 nonscrambled (ten actors (five males) \times two expressions (threat, neutral) \times two runs \times two repetitions) and 80 scrambled videos and 16 oddballs (inverted video clips)) which were presented in two runs in the MRI scanner. There were 80 null events (blank, green screen) with a duration of 2000 ms. These 176 stimuli and 80 null events were randomized within each run. A trial started with a fixation cross (500 ms), followed by a video (2000 ms) and a blank screen (2450 ms). An oddball task was used to control for attention and required participants to press a button each time an inverted video clip appeared so that trials of interest were uncontaminated by motor responses. Stimuli were back-projected onto a screen positioned behind the subject's head and viewed through a mirror attached to the head coil. Stimuli were centered on the display screen and subtended 11.4° of visual angle vertically for the body stimuli, and 7.9° of visual angle vertically for the face stimuli.

Procedure

Participants' head movements were minimized by an adjustable padded head-holder. Responses were recorded by an MR-compatible keypad, positioned on the right side of the participant's abdomen. After the two experimental runs, participants were given a functional localizer. Stimulus presentation of the main experiment and of the separate localizer study was controlled by using Presentation software (Neurobehavioral Systems, San Francisco, CA). After the scanning session, participants were guided to a quiet room where they were seated in front of a computer and validated the stimuli they had previously seen in the scanner by choosing between a threatening (fear or anger) or a neutral label.

fMRI data acquisition

Functional images were acquired using a 3.0-T Magnetom scanner (Siemens, Erlangen, Germany). For each participant, a three-dimensional

T1-weighted data encompassing the whole brain was acquired (scan parameters: repetition time (TR) = 2250 ms, echo time (TE) = 2.4 ms, flip angle (FA) = 9°, field of view (FOV) = 256 × 256 mm², matrix size = 256 × 256 mm, number of slices = 192, slice thickness = 1 mm, no gap, total scan time = 8 min, 5 s). Blood Oxygenation Level Dependent (BOLD) sensitive functional images were acquired using a gradient echo-planar imaging (EPI) sequence (TR = 2000 ms, TE = 30 ms, 32 transversal slices, descending interleaved acquisition, 3.5 mm slice thickness, with no interslice gap, FA = 90°, FOV = 224 mm, matrix size = 64 × 64 mm). An automatic shimming procedure was performed before each scanning session. A total of 645 functional volumes were collected for each participant plus a high-resolution T1-weighted anatomical scan (TR = 2250 ms, TE = 2.6 ms, 192 sagittal slices, voxel size 1 × 1 × 1 mm, FA = 9°, Inversion Time (TI) = 900 ms). The localizer scan parameters were as follows: TR = 2000 ms, TE = 30 ms, FA = 90°, matrix size = 256 × 256 mm, FOV = 256 mm, slice thickness = 2 mm (no gap), number of volumes = 310 (total scan time = ten minutes).

Statistical parametric mapping

Functional images were processed using the SPM2 software package (Wellcome Department of Imaging Neuroscience; see 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 639 functional images were reoriented to the anterior/posterior commissures (AC–PC) plane, slice time corrected to the middle slice and spatially realigned to the first volume, subsampled at an isotropic voxel size of 2 mm, normalized to the standard MNI space using the EPI reference brain and spatially smoothed with 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 SPM2.

At the first-level analysis, nine effects of interest were modeled: four represented trials where subjects perceived emotional expressions or neutral face and body videos, four represented the scrambled counterparts, and one represented the oddball condition. Null events were modeled implicitly. The BOLD response to the stimulus onset for each event type was convolved with the canonical haemodynamic response function over 2000 ms. For each subject's session, six covariates were included in order to capture residual movement-related artifacts (three rigid-body translations and three 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 cutoff frequency of 1/128 Hz. We smoothed the images of parameter estimates of the eight contrasts of interest with a 6-mm FWHM isotropic Gaussian kernel and estimated the following main effects and interactions at the first level:

- 1) Main effect of body vs. face [*Emotion + neutral (body vs. face)*];
- 2) Main effect of face vs. body [*Emotion + neutral (face vs. body)*];
- 3) Main effect of emotion vs. neutral [*Emotion vs. neutral (face + body)*]

At the second level of analysis, we performed between-subjects ANOVAs to isolate, in the main effects contrasts estimated at the first level, effects common to the fear and anger groups. Our goal was to study common modulations by threat in areas involved in processing faces and bodies, rather than studying specific modulations by fear and anger (see Pichon et al., 2009). Contrasts of main effects described above were entered in three between-subjects ANOVAs. The between factor corresponded here to group exposed to either fear or anger stimuli. A nonsphericity correction was applied for variance differences between conditions and subjects. Conjunction contrasts were estimated to reveal modulations common to both groups. For example, the ANOVA 'body vs. face' is a conjunction between the first-level contrasts 'body vs. face' estimated for subjects of Experiment 1 (anger) and Experiment 2 (fear). The conjunction allows

rejection of the null hypothesis only if all comparisons in the conjunction are individually significant (Friston et al., 2005).

Given the conservative analyses based on the conjunction null hypothesis, we displayed activations that survived a threshold of $T > 2.75$ ($p < .005$, uncorrected) with a minimum cluster extent of 20 contiguous voxels and report only p values that survived the threshold of $T > 3.39$ ($p < .001$, uncorrected) with a minimum cluster extent of ten contiguous voxels. In addition, we indicate in tables, peaks that survived false discovery rate (FDR) correction ($p < .05$) (Genovese et al., 2002). Statistical maps were overlaid on the SPM's single subject brain compliant with MNI space, i.e., Colin27 (Holmes et al., 1998) in the anatomy toolbox (www.fz-juelich.de/ime/spm_anatomy_toolbox, see Eickhoff et al. (2005) for a description). The atlas of Duvernoy was used for macroscopical labeling (Duvernoy, 1999).

Localization of face- and body-sensitive regions

Face- and body-sensitive voxels in the EBA, FFA/FBA, STS, AMG, and TPJ were identified using a separate localizer scan session in which participants performed a one backward task on face, body, house, and tool stimuli. The localizer consisted of 20 blocks of 12 trials of faces, bodies (neutral expressions, ten male, and ten female actors), objects, and houses (20 unique tools and 20 unique houses). Body pictures were selected from our large database of body expressions, and only the stimuli that were recognized as being absolutely neutral were included. To read more about the validation procedure of these stimuli, we refer the reader to the article of van de Riet et al. (2009). The tools (for example, pincers, a hairdryer etc.) and houses were selected from the Internet. All pictures were equal in size and were presented in a grayscale on a grey background. Stimuli were presented in a randomized blocked design and were presented for 800 ms with an ISI of 600 ms. Participants had to indicate whether the previous stimulus was the same as the one presented. We are currently preparing an extensive analysis of this localizer in a large sample of participants (van den Stock et al., in preparation).

Preprocessing was similar to the main experiment. At the first-level analysis, four effects of interest were modeled: faces, bodies, houses, and tools. For each subject's session, six covariates were included in order to capture residual movement-related artifacts (three rigid-body translations and three 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 cutoff frequency of 1/128 Hz. We smoothed the images of parameter estimates of the contrasts of interest with a 6-mm FWHM isotropic Gaussian kernel. At the group level, the following t -tests were performed: face > house, body > house, and, subsequently, a conjunction analysis [body > house AND face > house]. The resulting images were thresholded liberal ($p < .05$, uncorrected) to identify the following face- and body-sensitive regions of the brain: FFA/FBA, AMG, STS, and EBA (see Table 1 for coordinates and the contrasts used). ROIs were defined using a sphere with a radius of 5 mm centred onto the group peak activation of the localizer. We did not detect TPJ with our localizer. All chosen areas appeared in the whole brain analysis and are well known to process facial and bodily expressions (see Fig. 1). However, since there is a lot of discussion about using the same data set of the main experiment for the localization of specific areas to make ROIs (Kriegeskorte et al., 2009), we defined TPJ by averaging the group peaks from our former studies (Grèzes et al., 2007; Pichon et al., 2008, 2009). The MNI coordinates of these voxels are shown in Table 1.

The beta values of the ROIs were extracted for the following conditions: face threat, body threat, face neutral and body neutral. Since there were almost no differences across the left and right hemispheric ROIs and our interest does not concern hemispheric lateralization, we pool bilateral ROIs to reduce the total number of areas. Main and interaction effects were tested in SPSS in an ANOVA and were followed up with subsequent Bonferroni-corrected post-hoc 2-tailed t -tests.

Table 1
Coordinates used to create regions of interest.

Hemisphere	Anatomical region	MNI coordinates			Reference	Contrast
		x	y	z		
R	Fusiform face/body area	42	-46	-22	Localizer	[Body > house AND face > house]
L		-42	-46	-22	Localizer	Coordinate from right hemisphere
R	Amygdala	18	-4	-16	Localizer	Face > house
L		-18	-8	-20	Localizer	Face > house
R	Superior temporal sulcus	54	-52	18	Localizer	[Body > house AND face > house]
L		-54	-52	18	Localizer	Coordinate from right hemisphere
R	Extrastriate body area	52	-70	-2	Localizer	Body > house
L		-50	-76	6	Localizer	Body > house
R	Temporoparietal junction	62	-40	26	1 + 2 + 3	1 + 2 + 3
L		-60	-40	24	2 + 3	2 + 3

Average coordinate:

1. Grèzes et al., 2007 (fear body > neutral body).
2. Pichon et al., 2008 (anger body > neutral body).
3. Pichon et al., 2009 [anger body AND fear body].

Results

fMRI results

Bodies vs. faces

The conjunction between *body vs. face* [(anger + neutral (BO vs. FA)) and [fear + neutral (BO vs. FA))] yielded a large increase of activity in both hemispheres including the cuneus, middle occipital/temporal gyrus, inferior temporal gyrus, and TPJ extending to the paracentral lobule and the posterior cingulate gyrus. This cluster included the FBA, EBA, and STS regions that were found in the localizer experiment.

Other areas included the supramarginal gyrus, superior parietal lobule, left thalamus, primary somatosensory cortex (Brodmann area (BA) 3b/2), and intraparietal sulcus. The full list of activations is presented in Table 2 (see also Fig. 1).

Faces vs. bodies

The conjunction between *face vs. body* [(anger + neutral (FA vs. BO)) and [fear + neutral (FA vs. BO))] showed activations in the occipital pole, left hippocampus, and right AMG (see Table 3 and Fig. 1).

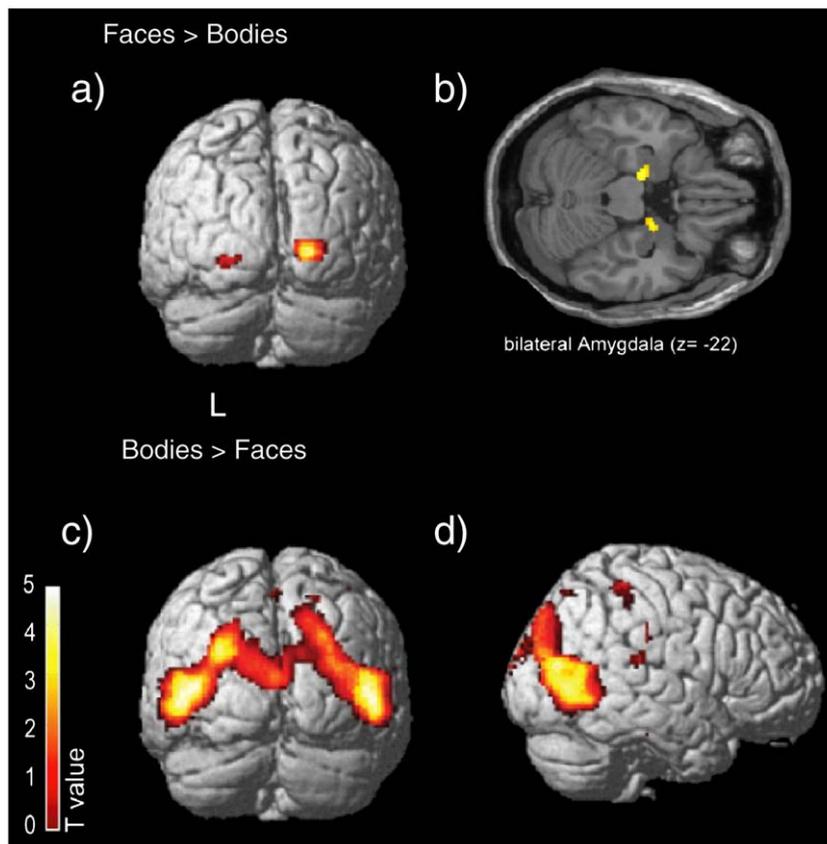


Fig. 1. Statistical maps of the whole brain analysis. Statistical maps at $p < .001$, uncorrected, with a minimum cluster extent of 10 voxels showing a) common brain areas to fearful and neutral faces vs. bodies and angry and neutral faces vs. bodies, rendered on the Colin brain (SPM) and b) superimposed on SPM standard single-subject T1-weighted coronal section. AMG is sensitive to facial expressions. c) Statistical maps showing common brain areas to fearful and neutral bodies vs. faces and angry and neutral bodies vs. faces, rendered on the Colin brain (SPM), coronal view and d) sagittal view. Parietal and temporal regions were specifically involved in body stimuli. Results are listed in Table 2 and 3.

Table 2
Body vs. face stimuli.

Hemisphere	Anatomical region	MNI coordinates			z value	Size in voxels	
		x	y	z			
L	Middle occipital gyrus	−40	−80	6	5.54	7511	
L/R	Middle temporal gyrus (MT/V5/EBA)	±50	−74	4	5.24/5.33	7511	↓
R	Cuneus, dorsal part	18	−86	46	4.20	7511	↓
L/R	Cuneus (BA 18)	±6	−92	16	4.93/5.11	7511	↓
R	Intraparietal sulcus, middle part	32	−84	22	4.88	7511	↓
L	Intraparietal sulcus, superior part	−22	−76	36	4.06	7511	↓
L/R	Fusiform/lingual gyrus	±26	−58	−10	3.73/4.19	56/7511	↓
R	Posterior middle cingulate cortex	12	−40	50	4.11	435	
L	Paracentral lobule (BA 4)	−6	−38	50	2.45	7511	↓
L/R	Posterior cingulate cortex	±16	−22	42	3.52/4.01	7511	↓
R	Postcentral sulcus (BA 3b/2)	34	−36	54	3.84	435	↓
L	Inferior parietal lobule (BA 2)	−30	−42	48	3.10	100	
L	Temporoparietal junction	−46	−38	20	3.75	140	
R	(OP1)	56	−30	18	3.53	46	
L	Supramarginal gyrus	−66	−32	20	3.23	12	
R	Supramarginal gyrus (TPJ)	58	−26	34	3.45	21	
L/R	Superior parietal lobule	±22	−72	56	3.01/3.23	129/18	
R	Inferior temporal gyrus	46	−24	−26	3.54	16	
L	Thalamus	−18	−28	4	3.46	40	
R	Inferior temporal gyrus	52	−58	−4	4.93	7511	↓
L		−52	−44	−20	3.03	41	

p < .001 uncorrected, extend threshold 10 voxels.
All results listed survived FDR correction *p* < .001.
↓ subpeak.

Emotion vs. neutral

The *emotion vs. neutral* conjunction [(anger vs. neutral (FA + BO)) AND [(fear vs. neutral (FA + BO))] showed bilateral activity in EBA and STS. Neither contrasting *anger vs. fear* (inclusively masked by anger vs. neutral, *p* = .05), nor *fear vs. anger* (inclusively masked by fear vs. neutral, *p* = .05) revealed significant activations (*p* = .001, uncorrected). See Table 4.

Facial and bodily expressions of emotion in different ROIs

To examine emotion effects in well known face- and body-selective areas, we extracted the beta values of predefined ROIs as described previously (see Fig. 2).

EBA. EBA showed a main effect of emotion ($F(1,25) = 45.343, p < .001, \eta_p^2 = .65$) and category ($F(1,25) = 154.853, p < .001, \eta_p^2 = .86$). This area was more active for threatening versus neutral expressions and for bodies than faces (both corrected, *p* < .001). EBA showed an interaction between category and emotion ($F(1,25) = 5.575, p < .05, \eta_p^2 = .18$). Both faces and bodies induced more activity when expressing a threatening versus a neutral expression (faces: $t(25) = 3.362, p < .005, d = .43$; bodies: $t(25) = 6.349, p < .001, d = .30$), yet the difference in bodies versus faces was larger ($t(25) = 11.501, p < .001, d = 1.46$).

FFA/FBA. FFA/FBA showed a main effect of emotion ($F(1,25) = 9.463, p < .005, \eta_p^2 = .28$). This area was more active for threatening than neutral expressions (corrected, *p* < .005), irrespective of the specific category.

Table 3
Face vs. body stimuli.

Hemisphere	Anatomical region	MNI coordinates			z value	Size in voxels
		x	y	z		
L/R	Occipital pole (BA 17)	±18	−100	0	3.46/4.98	48/225
L	Hippocampus	−14	−12	−22	3.3	47
R	Amygdala	20	−4	−22	3.20	28

p < .001, extended threshold 10 voxels.

STS. STS showed a main effect of emotion ($F(1,25) = 21.404, p < .001, \eta_p^2 = .46$) and category ($F(1,25) = 7.293, p < .05, \eta_p^2 = .23$). This area was more active for threatening versus neutral expressions (corrected, *p* < .001) and for bodies than faces (corrected, *p* < .05). STS showed an interaction between category and emotion ($F(1,25) = 7.874, p < .01, \eta_p^2 = .24$). Whereas STS did not differentially respond to emotional versus neutral faces (*p* = .265), activity was higher for emotional versus neutral bodies ($t(25) = 4.386, p < .005, d = .45$).

AMG. AMG showed a main effect of category ($F(1,25) = 18.568, p < .001, \eta_p^2 = .43$). This area was more active for faces than bodies (corrected, *p* < .001), irrespective of the emotional component.

TPJ. TPJ showed a main effect of category ($F(1,24) = 16.227, p < .001, \eta_p^2 = .39$) and emotion ($F(1,24) = 4.374, p < .05, \eta_p^2 = .15$). This area was more active for threatening than neutral expressions (corrected, *p* < .05) and for bodies than faces (corrected, *p* < .001).

Discussion

Our comparative study of the neurofunctional basis of perceiving video clips of facial and bodily expressions of threat (fear and anger) reveals similarities as well as differences between the neural basis of facial and bodily expression perception. The first major finding is that the AMG is more active for facial than for bodily expressions, but independently of the facial emotion. Secondly, a number of areas

Table 4
Emotional vs. neutral stimuli.

Hemisphere	Anatomical region	MNI coordinates			z value	Size in voxels
		x	y	z		
L/R	Middle occipital gyrus (MT/V5/EBA)	±50	−78	2	5.42	237
R	Superior temporal sulcus/gyrus	70	−38	14	4.22	128
L	Superior temporal sulcus/middle temporal gyrus	−46	−48	10	3.07	44

p < .001, extend threshold 10 voxels.

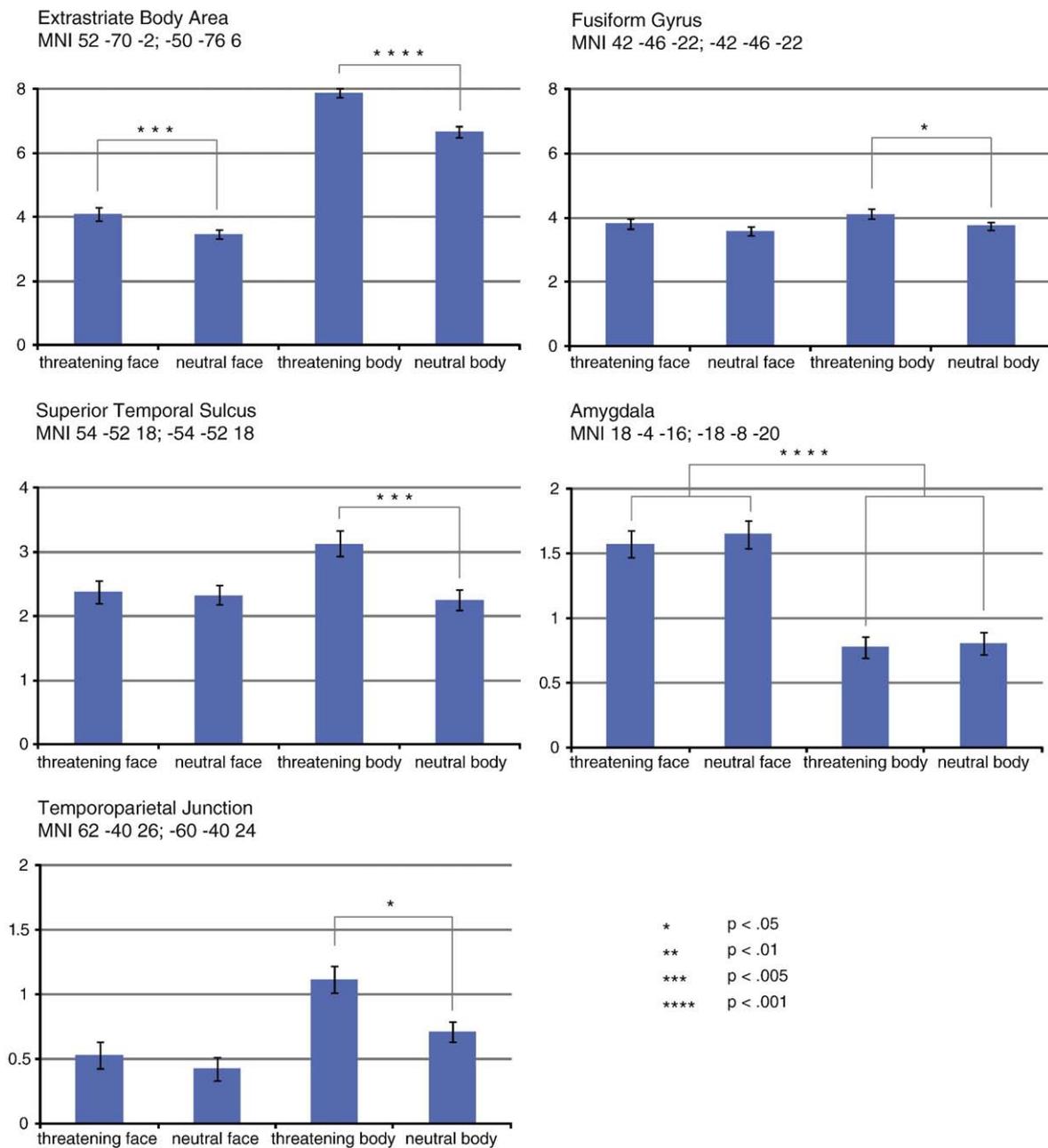


Fig. 2. Facial and bodily expressions of emotion. Please note the differences in scale. EBA was more active for threatening versus neutral expressions and for bodies than faces. Both faces and bodies induced more activity when expressing a threatening versus neutral emotion yet the difference in bodies versus faces was larger. FFA/FBA was more active for threatening than neutral expressions, irrespective of the specific category, yet only significant for the bodies. STS was more active for threatening versus neutral expressions and for bodies than faces. Whereas STS did not differentially respond to emotional versus neutral faces, activity was higher for emotional versus neutral bodies. AMG was more active for faces than bodies, irrespective of the emotional component. TPJ was more active for threatening than neutral expressions and for bodies than faces.

show higher activation for bodies than for faces. These are the cuneus, FG, EBA, TPJ, SPL, SI, as well as the thalamus. Thirdly, whereas EBA and STS show specific increased activity to threatening body expressions, FG responds equally to emotional faces and bodies.

Faces and amygdala activation

AMG was more active for facial than for bodily expressions. Our study provides the first direct comparison between dynamic facial and bodily expressions. The results show that AMG is responding to all face, and to a smaller extent, all body stimuli yet is not more sensitive to emotional than to neutral face videos. Other studies that used dynamic facial expressions did not find AMG activity either when contrasting emotional versus neutral faces (Grosbras and Paus, 2006;

Kilts et al., 2003; Puce and Perrett, 2003; Simon et al., 2006; Thompson et al., 2007; van der Gaag et al., 2007; Wheaton et al., 2004). Hurlmann et al. (2008) found two clusters (<15 voxels) in the left AMG for happy but not for angry versus neutral facial animations. Sato et al. (2004) found left AMG in an ROI analysis by contrasting fearful but not happy morphed faces versus a *mosaic pattern*. Trautmann et al. (2009) report more left AMG activity for dynamic disgusted but not happy versus neutral faces. In earlier studies using still images (Hadjikhani and de Gelder, 2003; van de Riet et al., 2009), we also found the AMG responding similarly to facial and bodily fear expressions. On the other hand, the AMG activity found here with dynamic stimuli is not specific for threatening facial expressions.

One explanation for the lack of strong statistical evidence for increased AMG involvement in dynamic fear and anger expressions is

that the difference between neutral and expressive faces may be smaller for dynamic than static stimuli. A dynamic neutral face has already by itself a strong social meaning. We know that AMG is responsive to ambiguity as exists when facial information is partly missing (Whalen et al., 1998; Hsu et al., 2005). In monkeys, increased AMG activity has been recorded during passive observation of social stimuli such as conspecifics facial expressions, gaze direction or social interactions (Logothetis et al., 1999; Gothard et al., 2007; Hoffman et al., 2007; Brothers et al., 1990). AMG activity is larger when during social communication with unpredictable consequences as compared to physical aggression (Kling et al., 1979). The BOLD response in AMG during the identity matching of neutral faces, was equally large as during matching the affect of faces (Wright and Liu, 2006). These studies suggest that the AMG response may be driven by neutral yet salient faces and fits with the notion that it encodes salience and modulates recognition and social judgment (Tsuchiya et al., 2009).

Body-specific activations and emotional body expressions

Recent fMRI studies using neutral stimuli have identified dedicated networks of face as well as of body-sensitive brain areas that are partly overlapping. STS as well as FG play a role in face as well as in body perception (for a review of currently available studies, see de Gelder et al., 2010). The role of FG in processing facial expressions is already well known, and evidence is accumulating that FG also plays a role in body perception. In line with our earlier studies with static stimuli (Meeren et al., 2008; van de Riet et al., 2009), we observe here that the FG is involved in processing dynamic bodies and faces. The sensitivity of FG to threat is not stimulus category specific. As expected, body videos trigger activity in EBA (Grèzes et al., 2007; Peelen and Downing, 2007; Pichon et al., 2008), especially when the expression was threatening. However, since the movement quantification method we used may not reflect the neural computation of movement, we cannot rule out that EBA reacts also to movement and threatening videos contained more movement than neutral videos.

TPJ is systematically associated with a variety of social cognitive tasks such as perspective-taking (Ruby and Decety, 2003), empathy (Jackson et al., 2006; Lamm et al., 2007), and theory of mind (Lawrence et al., 2006; Saxe and Wexler, 2005; for a review, see Decety and Lamm, 2007). In the current study, TPJ, although responsive to all social stimuli, was more responsive to bodies than to faces, and especially bodily expressions of emotion which is in line with our earlier studies (Grèzes et al., 2007; Pichon et al., 2008, 2009). It is not surprising that TPJ reacts more to bodies than to faces since bodily expressions, in contrast to facial expressions, imply action (de Gelder et al., 2004; de Gelder, 2006; 2010). TPJ is known to be involved in action understanding (Samson et al., 2004). Interestingly, Ruby and Decety (2001) observed greater TPJ activation when participants imagined another person performing an action than imagining themselves performing the action. The observed increased activity for bodily expressions, especially emotional ones, fits well with the literature on action understanding.

Conclusion

Our study yielded several important findings. The AMG was modulated more by faces than bodies. A number of crucial areas showed higher activation for bodies than for faces and some reflected affective stimulus meaning. Body specific activation increases were found in the FG, EBA, SPL, SI, thalamus, and TPJ. TPJ and FG showed more activity while processing emotional faces and bodies than neutral ones. There was an interaction between category selectivity and emotion in EBA and in STS. This area was specifically modulated by threatening body expressions. So, whereas EBA and STS show a specific activity pattern triggered by emotional bodies, FG is equally responsive to emotional faces and bodies. Altogether our findings

underscore the importance of including investigations using bodily expressions for a better understanding of the neural basis of affective processes.

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References

- Allison, T., Puce, A., McCarthy, G., 2000. Social perception from visual cues: role of the STS region. *Trends Cogn. Sci.* 4, 267–278.
- Bonda, E., Petrides, M., Ostry, D., Evans, A., 1996. Specific involvement of human parietal systems and the amygdala in the perception of biological motion. *J. Neurosci.* 16, 3737–3744.
- Brothers, L., Ring, B., Kling, A., 1990. Response of neurons in the macaque amygdala to complex social stimuli. *Behav. Brain Res.* 41 (3), 199–213.
- de Gelder, B., 2006. Towards the neurobiology of emotional body language. *Nat. Rev. Neurosci.* 7 (3), 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. *Proc. Natl Acad. Sci. USA* 101 (47), 16701–16706.
- de Gelder, B., Van den Stock, J., Meeren, H.K.M., Sinke, C.B.A., Kret, M.E., Tamiotto, M., 2010. Standing up for the body. Recent progress in uncovering the networks involved in processing bodies and bodily expressions. *Neurosci. Biobehav. Rev.* 34, 513–527.
- Decety, J., Lamm, C., 2007. The role of the right temporoparietal junction in social interaction: how low-level computational processes contribute to meta-cognition. *Neuroscientist* 13 (6), 580–593.
- Downing, P.E., Jiang, Y., Shuman, M., Kanwisher, N., 2001. A cortical area selective for visual processing of the human body. *Science* 293 (5539), 2470–2473.
- Duvernoy, H.M., 1999. *The Human Brain: Surface, Three-dimensional Sectional Anatomy with MRI, and Blood Supply*. Springer Verlag, Wien New York.
- Eickhoff, S.B., Stephan, K.E., Mohlberg, H., Grefkes, C., Fink, G.R., Amunts, K., Zilles, K., 2005. A new SPM toolbox for combining probabilistic cytoarchitectonic maps and functional imaging data. *Neuroimage* 25 (4), 1325–1335.
- Friston, K., Holmes, A.P., Worsley, K., Poline, J., Frith, C., Frackowiak, R., 1995. Statistical parametric maps in functional imaging: a general linear approach. *Hum. Brain Mapp.* 2 (4), 189–210.
- Friston, K.J., Penny, W., David, O., 2005. Modeling brain responses. *Int. Rev. Neurobiol.* 66, 89–124.
- Gauthier, I., Skudlarski, P., Gore, J.C., Anderson, A.W., 2000. Expertise for cars and birds recruits brain areas involved in face recognition. *Nature Neuroscience* 3 (2), 191–197.
- Genovesi, C.R., Lazar, N.A., Nichols, T., 2002. Thresholding of statistical maps in functional neuroimaging using the false discovery rate. *Neuroimage* 15 (4), 870–878.
- Gothard, K.M., Erickson, Spitzer, K.S., Amaral, D.G., 2007. Neural responses to facial expression and face identity in the monkey amygdala. *J. Neurophysiol.* 97 (2), 1671–1683.
- Grèzes, J., Pichon, S., de Gelder, B., 2007. Perceiving fear in dynamic body expressions. *Neuroimage* 35 (2), 959–967.
- Grosbras, M.H., Paus, T., 2006. Brain networks involved in viewing angry hands or faces. *Cereb. Cortex* 16 (8), 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. *Curr. Biol.* 13 (24), 2201–2205.
- Haxby, J.V., Hoffman, E.A., Gobbini, M.I., 2000. The distributed human neural system for face perception. *Trends Cogn. Sci.* 4, 223–233.
- Hodzic, A., Kaas, A., Muckli, L., Stirn, A., Singer, W., 2009. Distinct cortical networks for the detection and identification of human body. *Neuroimage* 45, 1264–1271.
- Hoffman, K.L., Gothard, K.M., Schmid, M.C., Logothetis, N.K., 2007. Facial-expression and gaze-selective responses in the monkey amygdala. *Curr. Biol.* 17, 766–772.
- Holmes, C.J., Hoge, R., Collins, L., Woods, R., Toga, A.W., Evans, A.C., 1998. Enhancement of MR images using registration for signal averaging. *J. Comput. Assist. Tomogr.* 22 (2), 324–333.
- Hsu, M., Bhatt, M., Adolphs, R., Tranel, D., Camerer, C.F., 2005. Neural systems responding to degrees of uncertainty in human decision-making. *Science* 30, 1680–1683.
- Hurlmann, R., Rehme, A.K., Diessel, M., Kukulja, J., Maier, W., Walter, H., Cohen, M.C., 2008. Segregating intra-amygdalar responses to dynamic facial emotion with cytoarchitectonic maximum probability maps. *J. Neurosci. Methods* 172 (1), 13–20.
- Jackson, P.L., Brunet, E., Meltzoff, A.N., Decety, J., 2006. Empathy examined through the neural mechanisms involved in imagining how I feel versus how you feel pain: an event-related fMRI study. *Neuropsychologia* 44, 752–761.
- Kanwisher, N., McDermott, J., Chun, M.M., 1997. The fusiform face area: a module in human extrastriate cortex specialized for face perception. *J. Neurosci.* 17 (11), 4302–4311.

- 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 (1), 156–168.
- Kling, A., Steklis, H.D., Deutsch, S., 1979. Radiotelemetered activity from the amygdala during social interactions in the monkey. *Exp. Neurol.* 66 (1), 88–96.
- Kriegeskorte, N., Simmons, W.K., Bellgowan, P.S.F., Baker, C.I., 2009. Circular analysis in systems neuroscience—the dangers of double dipping. *Nat. Neurosci.* 5, 535–540.
- Lamm, C., Decety, J., 2008. Is the extrastriate body area (EBA) sensitive to the perception of pain in others? *Cereb. Cortex* 18, 2369–2373.
- Lamm, C., Batson, C.D., Decety, J., 2007. The neural basis of human empathy—effects of perspective-taking and cognitive appraisal. *J. Cogn. Neurosci.* 19, 1–7.
- Lawrence, E.J., Shaw, P., Giampietro, V.P., Surguladze, S., Brammer, M.J., David, A.S., 2006. The role of ‘shared representations’ in social perception and empathy: an fMRI study. *Neuroimage* 29, 1173–1184.
- Logothetis, N.K., Guggenberger, H., Peled, S., Pauls, J., 1999. Functional imaging of the monkey brain. *Nat. Neurosci.* 2, 555–562.
- Meeren, H.K., Hadjikhani, N., Ahlfors, S.P., Hamalainen, M.S., de Gelder, B., 2008. Early category-specific cortical activation revealed by visual stimulus inversion. *PLoS ONE* 3 (10), e3503.
- Peelen, M.V., Downing, P.E., 2005. Selectivity for the human body in the fusiform gyrus. *J. Neurophysiol.* 93 (1), 603–608.
- Peelen, M.V., Downing, P.E., 2007. The neural basis of visual body perception. *Nat. Rev. Neurosci.* 8 (8), 636–648.
- Peelen, M.V., Glaser, B., Vuilleumier, P., Eliez, S., 2007. Differential development of selectivity for faces and bodies in the fusiform gyrus. *Dev. Sci.* 12 (6), F16–F25.
- Peelen, M.V., Atkinson, A.P., Andersson, F., Vuilleumier, P., 2007. Emotional modulation of body-selective visual areas. *Soc. Cogn. Affect. Neurosci.* 2, 274–283.
- Perrett, D.I., Harries, M.H., Bevan, R., Thomas, S., Benson, P.J., Mistlin, A.J., Chitty, A.J., Hietanen, J.K., Ortega, J.E., 1989. Frameworks of analysis for the neural representation of animate objects and actions. *J. Exp. Biol.* 146, 87–113.
- Pichon, S., de Gelder, B., Grèzes, J., 2008. Emotional modulation of visual and motor areas by still and dynamic body expressions of anger. *Soc. Neurosci.* 3 (3), 199–212.
- Pichon, S., de Gelder, B., Grèzes, J., 2009. Two different faces of threat. Comparing the neural systems for recognizing fear and anger in dynamic body expressions. *Neuroimage* 47 (4), 1873–1883.
- Puce, A., Perrett, D., 2003. Electrophysiology and brain imaging of biological motion. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 358 (1431), 435–445.
- Puce, A., Allison, T., Asgari, M., Gore, J.C., McCarthy, G., 1996. Differential sensitivity of human visual cortex to faces, letterstrings, and textures: a functional magnetic resonance imaging study. *Journal of Neuroscience* 16 (16), 5205–5215.
- Ruby, P., Decety, J., 2001. Effect of the subjective perspective taking during simulation of action: a PET investigation of agency. *Nat. Neurosci.* 4, 546–550.
- Ruby, P., Decety, J., 2003. What you believe versus what you think they believe? A neuroimaging study of conceptual perspective taking. *Eur. J. Neurosci.* 17, 2475–2480.
- Samson, D., Apperly, I.A., Chiavarino, C., Humphreys, G.W., 2004. Left temporoparietal junction is necessary for representing someone else’s belief. *Nat. Neurosci.* 7, 499–500.
- 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. *Cogn. Brain Res.* 20, 81–91.
- Saxe, R., Wexler, A., 2005. Making sense of another mind: the role of the right temporoparietal junction. *Neuropsychologia* 43, 1391–1399.
- Simon, D., Craig, K.D., Miltner, W.H., Rainville, P., 2006. Brain responses to dynamic facial expressions of pain. *Pain* 126 (1–3), 309–318.
- Taylor, J.C., Wiggett, A.J., Downing, P.E., 2007. Functional MRI analysis of body and body part representations in the extrastriate and fusiform body areas. *J. Neurophysiol.* 98, 1626–1633.
- Thompson, J.C., Clarke, M., Stewart, T., Puce, A., 2005. Configural processing of biological motion in human superior temporal sulcus. *J. Neurosci.* 25, 9059–9066.
- Thompson, J.C., Hardee, J.E., Panayiotou, A., Crewther, D., Puce, A., 2007. Common and distinct brain activation to viewing dynamic sequences of face and hand movements. *Neuroimage* 37 (3), 966–973.
- Tsuchiya, N., Moradi, F., Felsen, C., Yamazaki, M., Adolphs, R., 2009. Intact rapid detection of fearful faces in the absence of the amygdala. *Nat. Neurosci.* 12, 1224–1225.
- Trautmann, S.A., Fehr, T., Herrmann, M., 2009. Emotions in motion: dynamic compared to static facial expressions of disgust and happiness reveal more widespread emotion-specific activations. *Brain Res.* 1284, 100–115.
- Urgesi, C., Calvo-Merino, B., Haggard, P., Aglioti, S.M., 2007. Transcranial magnetic stimulation reveals two cortical pathways for visual body processing. *J. Neurosci.* 27, 8023–8030.
- Van de Riet, W.A.C., Grèzes, J., de Gelder, B., 2009. Specific and common brain regions involved in the perception of faces and bodies and the representation of their emotional expressions. *Soc. Neurosci.* 4 (2), 101–120.
- Van den Stock, J., Sinke, C.B.A., Kret, M.E., de Gelder, B., in preparation. Individual differences in face and body perception brain areas.
- Van der Gaag, C., Minderaa, R.B., Keysers, C., 2007. Facial expressions: what the mirror neuron system can and cannot tell us. *Soc. Neurosci.* 2 (3–4), 179–222.
- Whalen, P.J., Rauch, S.L., Etcoff, N.L., McInerney, S.C., Lee, M.B., Jenike, M.A., 1998. Masked presentations of emotional facial expressions modulate amygdala activity without explicit knowledge. *J. Neurosci.* 18 (1), 411–418.
- Wheaton, K.J., Thompson, J.C., Syngienotis, A., Abbott, D.F., Puce, A., 2004. Viewing the motion of human body parts activates different regions of premotor, temporal, and parietal cortex. *Neuroimage* 22 (1), 277–288.
- Wright, P., Liu, Y., 2006. Neutral faces activate the amygdala during identity matching. *Neuroimage* 15 (29 (2)), 628–638.