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 processes are involved in 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 faces and bodies alike. EBA and superior temporal sulcus (STS) were more activated by threatening bodies.

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 underlying whole body perception partly overlaps with the functional role of body and face selective areas. A body-sensitive area 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 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 face 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; Hódzic 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
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 fearful 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 configurational 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 with 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 15 seconds. From each subject, a separate localizer study was controlled by using Presentation software (Neurobehavioral Systems, San Francisco, CA). After the scanning session, participants were given a functional localizer. This consisted of five different pictures (neutral, angry, fearful, happy, sad) which were presented in three runs in the fMRI scanner. 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 asked to rate how threatening or disgusting the stimuli were on a scale ranging from 1 to 5.

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 LevelDependent (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.filion.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 nonspecificity 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 pooled bilateral ROIs to reduce the total number of areas. Main and interaction effects were tested in SPMs in an ANOVA and were followed up with subsequent Bonferroni-corrected post-hoc 2-tailed t-tests.
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).

Table 1
Coordinates used to create regions of interest.

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

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].

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.

<table>
<thead>
<tr>
<th>Hemisphere</th>
<th>Anatomical region</th>
<th>MNI coordinates</th>
<th>z value</th>
<th>Size in voxels</th>
</tr>
</thead>
<tbody>
<tr>
<td>L/R</td>
<td>Middle occipital gyrus</td>
<td>-40 -80 6 5.54  7511</td>
<td></td>
<td></td>
</tr>
<tr>
<td>L/R</td>
<td>Middle temporal gyrus (MT/V5/EBA)</td>
<td>±50 74 4 5.24 733 7511</td>
<td></td>
<td></td>
</tr>
<tr>
<td>R</td>
<td>Cuneus, dorsal part</td>
<td>18 -86 46 4.20 7511</td>
<td></td>
<td></td>
</tr>
<tr>
<td>L/R</td>
<td>Cuneus (BA 18)</td>
<td>±6 -92 16 4.93 5.11 7511</td>
<td></td>
<td></td>
</tr>
<tr>
<td>R</td>
<td>Intraparietal sulcus, middle part</td>
<td>-22 -84 22 4.88 7511</td>
<td></td>
<td></td>
</tr>
<tr>
<td>L/R</td>
<td>Intraparietal sulcus, superior part</td>
<td>±26 -58 -10 3.73 4.19 56/7511</td>
<td></td>
<td></td>
</tr>
<tr>
<td>R</td>
<td>Fusiform/lingual gyrus</td>
<td>12 -40 50 4.17 435</td>
<td></td>
<td></td>
</tr>
<tr>
<td>L/R</td>
<td>Posterior middle cingulate cortex</td>
<td>-6 -38 50 2.45 7511</td>
<td></td>
<td></td>
</tr>
<tr>
<td>R</td>
<td>Paracentral lobule (BA 4)</td>
<td>±16 -22 42 3.52 4.01 7511</td>
<td></td>
<td></td>
</tr>
<tr>
<td>L</td>
<td>Postcentral sulcus (BA 3b/2)</td>
<td>34 -36 54 3.84 435</td>
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<tr>
<td>L/R</td>
<td>Inferior parietal lobule (BA 2)</td>
<td>-30 -42 48 3.10 100</td>
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<td></td>
</tr>
<tr>
<td>L/R</td>
<td>Temporoparietal junction</td>
<td>-46 -38 29 3.75 140</td>
<td></td>
<td></td>
</tr>
<tr>
<td>R</td>
<td>(OP1)</td>
<td>56 -30 18 3.53 46</td>
<td></td>
<td></td>
</tr>
<tr>
<td>L</td>
<td>Supramarginal gyrus</td>
<td>-66 -32 20 3.23 12</td>
<td></td>
<td></td>
</tr>
<tr>
<td>R</td>
<td>Supramarginal gyrus (TPJ)</td>
<td>58 -26 34 3.45 21</td>
<td></td>
<td></td>
</tr>
<tr>
<td>L/R</td>
<td>Superior parietal lobule</td>
<td>±22 -72 26 3.54 16</td>
<td></td>
<td></td>
</tr>
<tr>
<td>R</td>
<td>Inferior temporal gyrus</td>
<td>46 -24 -26 3.54 16</td>
<td></td>
<td></td>
</tr>
<tr>
<td>L</td>
<td>Thalamus</td>
<td>-18 -28 4 3.46 40</td>
<td></td>
<td></td>
</tr>
<tr>
<td>L</td>
<td>Inferior temporal gyrus</td>
<td>52 -58 -4 4.93 7511</td>
<td></td>
<td></td>
</tr>
<tr>
<td>L</td>
<td>-52 -44 -20 3.03 41</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

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, ηp² = .65) and category (F(1,25) = 154.853, p<.001, ηp² = .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, ηp² = .24). 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).

FPA/EBA. FPA/EBA showed a main effect of emotion (F(1,25) = 9.463, p<.005, ηp² = .28). This area was more active for threatening than neutral expressions (corrected, p<.005), irrespective of the specific category.

STS. STS showed a main effect of emotion (F(1,25) = 21.404, p<.001, ηp² = .46) and category (F(1,25) = 7.293, p<.05, ηp² = .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, ηp² = .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, ηp² = .43). This area was more active for faces than bodies (corrected, p<.001), irrespective of the emotional component.

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 3

Face vs. body stimuli.

<table>
<thead>
<tr>
<th>Hemisphere</th>
<th>Anatomical region</th>
<th>MNI coordinates</th>
<th>z value</th>
<th>Size in voxels</th>
</tr>
</thead>
<tbody>
<tr>
<td>L/R</td>
<td>Occipital pole (BA 17)</td>
<td>±18 -100 0 3.46 4.98 48/225</td>
<td></td>
<td></td>
</tr>
<tr>
<td>L</td>
<td>Hippocampus</td>
<td>-14 -12 -22 3.3 47</td>
<td></td>
<td></td>
</tr>
<tr>
<td>R</td>
<td>Amygdala</td>
<td>-20 -4 -22 3.2 28</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

p<.001, extended threshold 10 voxels.

Table 4

Emotional vs. neutral stimuli.

<table>
<thead>
<tr>
<th>Hemisphere</th>
<th>Anatomical region</th>
<th>MNI coordinates</th>
<th>z value</th>
<th>Size in voxels</th>
</tr>
</thead>
<tbody>
<tr>
<td>L/R</td>
<td>Middle occipital gyrus (MT/V5/EBA)</td>
<td>±50 -78 2 5.42 237</td>
<td></td>
<td></td>
</tr>
<tr>
<td>R</td>
<td>Superior temporal sulcus gyrus</td>
<td>70 -38 14 4.22 128</td>
<td></td>
<td></td>
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<tr>
<td>L</td>
<td>Superior temporal sulcus/middle temporal gyrus</td>
<td>-46 -48 10 3.07 44</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

p<.001, extend threshold 10 voxels.
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 (Grossbras 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). Hurlemann 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; Gotard 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 BA (Grèzes et al., 2007; Peele 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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