

Facial expressions: What the mirror neuron system can and cannot tell us

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Facial expressions contain both motor and emotional components. The inferior frontal gyrus (IFG) and posterior parietal cortex have been considered to compose a mirror neuron system (MNS) for the motor components of facial expressions, while the amygdala and insula may represent an “additional” MNS for emotional states. Together, these systems may contribute to our understanding of facial expressions. Here we further examine this possibility. In three separate event-related fMRI experiments, subjects had to (1) observe (2) discriminate and (3) imitate facial expressions. Stimuli were dynamic neutral, happy, fearful and disgusted facial expressions, and in Experiments 1 and 2, an additional pattern motion condition. Importantly, during each experiment, subjects were unaware of the nature of the next experiments. Results demonstrate that even passive viewing of facial expressions activates a wide network of brain regions that were also involved in the execution of similar expressions, including the IFG/insula and the posterior parietal cortex. Only a subset of these regions responded more during the observation of facial than pattern motion (bilateral ventral IFG, bilateral STS/MTG, bilateral amygdala, SMA). While the viewing of facial expressions recruited similar brain regions in all three experiments, adding an active task (discrimination, imitation) augmented the magnitude of these activations. Brain activations reflected differences in observed facial expressions, with emotional expressions activating relatively more the insula/frontal operculum, and neutral ones (blowing up the cheeks) the somatosensory cortices (SII). Using movies, fear activated the amygdala and disgust the insula, but other emotions activated these structures to a similar degree.

INTRODUCTION

Understanding the emotional facial expressions of others is important for daily social functioning. A number of different approaches have been used to investigate the way we understand the emotions of other people. Lesion studies looked at the consequences of damage to specific brain sites on the capacity to read the emotions of others (see Adolphs, Damasio, Tranel, Cooper, & Damasio,

2000, for the most extensive study). They found that damage to the right somatosensory cortex impaired subjects in recognizing basic emotions from visually presented facial expressions. According to Adolphs et al. (2000), this finding supports the idea that emotion recognition is mediated by a simulation mechanism within the observer, which generates somatosensory representations as if the observer feels similar emotional states to the ones being observed.

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More recently, the understanding of other people through facial expressions has been studied through the mirror neuron system (MNS). The critical property of this system is that the observation of a particular action activates regions involved in the execution of that particular action. Both in monkeys and humans, a vast literature exists describing the classical MNS to be composed of the posterior parietal cortex and the premotor cortex (BA 6/BA 44; e.g., Rizzolatti & Craighero, 2004; Rizzolatti, Fogassi, & Gallese, 2001). The superior temporal sulcus (STS) is closely related to the classical mirror neuron system in terms of function and connections but lacking clear motor properties (Gazzola, Aziz-Zadeh, & Keysers, 2006; Keysers & Gazzola, 2006).

Classically, the mirror-neuron matching system has been investigated through transitive, goal-directed actions. Facial expressions are a specific class of actions, not directed at a particular object, although facial expressions can be viewed as instrumental devices to influence other people (e.g., Blair, 2003; Russell, Bachorowski, & Fernandez-Dols, 2003), which in a sense is goal directed. Interestingly, neurons in the monkey's ventral premotor cortex (F5) have been described as responding to the observation of communicative mouth actions (Ferrari, Gallese, & Rizzolatti, 2003).

In humans, non-invasive neuroimaging techniques like fMRI have been applied to study the involvement of the MNS in the understanding of facial expressions. One fMRI approach required subjects in alternating blocks to observe facial expressions and to imitate them (Carr, Iacoboni, Dubeau, Mazziotta, & Lenzi, 2003; Dapretto et al., 2006). The blocks of facial expression observation consisted of a mix of static displays of several basic emotions. Results showed that premotor and parietal cortex were both involved in facial expression observation *and* execution, supporting the idea of the involvement of the MNS in understanding facial expressions. In addition, Carr et al. (2003) showed that two limbic regions, the amygdala and insula, were involved in both the observation and execution of facial expressions. Next, Leslie, Johnson-Frey, and Grafton (2004) used a paradigm in which subjects had to observe and imitate hand and face actions (smile and frown condition) using film clips instead of static displays. The right ventral premotor cortex was commonly activated during observation and imitation of facial expressions.

A study by Hennenlotter et al. (2005) specifically looked into the MNS involvement during the production and observation of pleasant affect (smiling). Right premotor cortex and inferior frontal cortex were involved in both conditions, in addition to right parietal operculum (SII) and left anterior insula. Considering only these studies, it is still an open question whether activated regions are confounded by the upcoming execution part of the study, as subjects knew they had to either imitate (Carr et al., 2003; Dapretto et al., 2006; Leslie et al., 2004) or to execute similar movements (Hennenlotter et al., 2005) subsequently. Reported MNS activations may thus reflect a preparatory state for future execution, and may therefore differentiate from naturalistic situations.

Another approach to studying the involvement of the MNS during facial expression observation is to use emotion *experiencing* and emotion *observation*. When subjects observed and experienced the emotion "disgust", Wicker et al. (2003) found the anterior insula and the anterior cingulate gyrus to be involved in both cases. These regions are located outside the classical MNS. Some of the overlapping anterior insula regions extended into the inferior frontal regions, although not in BA 44/BA 45. This finding supports the idea that humans have both a "classical" MNS for goal-directed actions (parietal and premotor regions) and an "extended" MNS for emotional states (insula, anterior cingulate cortex and, potentially, other brain regions). For the latter, the term "mirror neuron system" is used in an extended context, where neurons do not require visual and motor properties, but visual properties and matching properties in another domain—emotions or sensations (Keysers & Gazzola, 2006; Gallese, Keysers, & Rizzolatti, 2004). In order to understand further the respective contribution of these two mirror neuron systems involved in the processing of facial expressions, the observation of facial expressions can thus be combined with either an emotional experiencing paradigm to place the emphasis on the extended MNS or with a facial expression production paradigm to emphasize the classical MNS. This distinction bears a relation to the distinction found in psychological theories of emotion processing. Theories positing that understanding other people's emotions requires the induction of a similar *emotional* state in the observer would predict an important role for the extended MNS while theories positing that the production of a facial expression similar to the

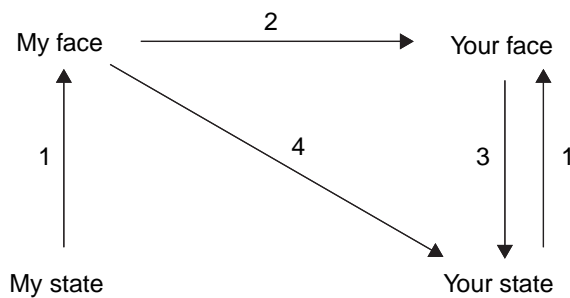


Figure 1. Empathy through simulation: possible processes that explain the sharing of feelings. Hypothesized processes are reflected by numbered arrows, which reflect the direction of influence: (1) Both your and my feeling state is reflected by a congruent facial expression; (2) The mimicry process by which your facial musculature reflects my facial expression; (3) Emotional contagion through a facial feedback mechanism causes the configuration of your facial musculature to initiate a congruent feeling state; (4) Direct contagion of my emotional state when you observe my facial expression: an alternative mechanism for empathy through mimicry and facial feedback mechanisms. Notice that after the direct contagion of an emotional state your face can also reflect this state (1). Psychological theories of understanding other people’s emotions differ in the causal relationship they see between sharing the emotional state and sharing the facial expression of others. Lipps (1907) posited that the observer automatically imitates the observed facial expression—facial mimicry (McIntosh, 1996), and that this mimicry is essential for understanding the emotion. Through facial feedback, the mimicked facial expression then leads to the experience of the emotion in the observer (indirect emotional contagion). Hess, Philippot, and Blairy (1998) on the other hand posited that observing the facial expression leads to the induction of a similar emotional state in the observer without the need for mimicry. Mimicry can then occur at a later point, as a reflection of the shared emotional state, but social context greatly modulates this process. Most theories lie somewhere between these two standpoints. Although some theories make clear predictions about what should come first—sharing the facial expression or the emotional state—the temporal resolution of fMRI is unsuited for resolving this difference reliably.

What is the relationship of these psychological models and the MNS? Lipps’ model is in tight relationship with motor mirror neurons, as they could provide a neural basis for the facial mimicry. Hess’s model on the other hand attributes a marginal role to motor mirror neurons. Her model predicts the existence of mirror neurons for emotional states, that would be involved both in emotion experience and emotion observation (see Keysers & Perrett, 2004). Such “emotional” mirror neurons have never been recorded in monkeys, but fMRI experiments suggests that they might exist, as voxels in the human brain show this property (Singer et al., 2004; Wicker et al., 2003). For a model that also adds reflective brain regions involved in Theory of Mind processes to the understanding of facial expressions see Keysers and Gazzola (2007).

observed is an essential component for emotion understanding (“facial feedback mechanism”) would predict an important role for the classical MNS (see Figure 1).

A reason for caution with a “facial expression-production” approach is that one might assume that with the mere production of a particular emotional expression one can find brain regions involved in both the motor part of a facial expression *and* the emotional state (e.g., by means of a facial feedback mechanism), and as a consequence find emotional-related brain structures. A more careful viewpoint is that through the execution of a facial expression one can only state something about the motor part of facial expressions and not the emotional state. This is in fact what previous studies using an imitation paradigm argue, that action representation in premotor cortex during facial expression observation mediates emotional recognition (Carr et al., 2003; Hennenlotter et al., 2005; Leslie et al., 2004).

The emotion specificity of the MNS has received limited attention. While Carr et al. (2003) explicitly excluded emotion specificity by mixing all emotions in imitation blocks, Hennenlotter et al. (2005) looked only at one emotion (smiling). The only study that investigated multiple emotions (disgust and pleasure) was performed by Wicker et al. (2003), although they only studied one positive and one negative emotion. One region commonly activated in all of these studies was the anterior insula, which has strong associations with disgust processing (Calder, Keane, Manes, Antoun, & Young, 2000). This leaves us wondering whether the anterior insula activation found by Carr et al. (2003) is specifically related to disgust processing or is commonly shared by several emotions within their paradigm as suggested by Jabbi, Swart, and Keysers (2007). Another limbic region showing mirror neuron properties in the Carr study was the amygdala. Data from animal studies and lesion patients have shown the importance of this structure in fear processing (Adolphs et al., 1999; Calder, Lawrence, & Young, 2001; LeDoux, 2000). The amygdala activations in the Carr study could therefore be exclusively related to fear processing. Alternatively, these activations may reflect the processing of multiple emotions as suggested by a number of previous studies (e.g., Fitzgerald, Angstadt, Jelsone, Nathan, & Phan, 2005; Van der Gaag, Minderaa, & Keysers, 2007; Winston, O’Doherty, & Dolan, 2003; Yang et al., 2002).

In this experiment, we will study the MNS with a “production” paradigm using a similar imitation task to that performed by Carr et al. (2003),

therefore being able to compare results. In an attempt to contribute to the understanding of facial expressions through mirroring, adjustments were made to the stimuli and paradigm to increase ecological validity and to be able to answer remaining questions: (a) Does the MNS become spontaneously active when observing facial expressions, even when subjects do not need to execute facial expressions? (b) Do different task instructions during the viewing of facial expressions change the pattern of activations in the MNS? (c) Is there biological motion specificity within the mirror neuron circuit? (d) Are the individual emotional facial expressions treated differently and/or specifically within the classical MNS? (e) Are the involvement of the insula and the amygdala during facial expression observation and production emotion specific? To answer these questions, subjects first had to passively observe in an event-related design *dynamic* neutral, disgusted, fearful and happy facial expressions. Prototypical examples of the mentioned basic emotions were used, as they are most likely to be associated with specific brain areas. An extra control condition comprised of pattern motion was included to be able to investigate biological motion specificity in the MNS. Next, subjects had to perform a delayed-match-to-sample task on the same movies. Finally, they were asked to imitate the four facial expressions. Important in this fixed-order experiment, subjects were unaware of the tasks to come.

If the observation and production of facial expressions in our experiment triggered an internal feeling of specific emotions, based on results of previous observation and/or experiencing studies on specific emotions, we expected to find categorical mirror activity for disgust in the anterior insula/frontal operculum (IFO), anterior cingulate and/or basal ganglia (Calder et al., 2000; Goldman & Sripada, 2005; Hennenlotter et al., 2004; Wicker et al., 2003) and for fear in the amygdala (Calder et al., 2000; Goldman & Sripada, 2005; Phan, Wager, Taylor, & Liberzon, 2002). Two meta-analyses did not find brain specificity for happiness (Murphy, Nimmo-Smith, & Lawrence, 2003; Phan et al., 2002), although two other studies found some evidence for specificity for happiness in the supplementary motor area (Fried, Wilson, MacDonald, & Behnke, 1998; Krolak-Salmon et al., 2006).

If, on the other hand, emotional states are not triggered by facial expressions we predicted that

ventral premotor regions would be activated equally by the different facial expressions.

MATERIALS AND METHODS

Subjects

Seventeen healthy young adults (age range 19–27 years of age; mean age 23.3 years; 9 women, 8 men) were recruited from the University of Groningen community. All subjects were right-handed (assessed with the Edinburgh Handedness Questionnaire; Oldfield, 1971) and were screened for neurological and psychiatric diseases. Informed consent was obtained from each subject in accordance with the human subjects research protocol approved by the Medical Ethical Committee of the University Medical Center Groningen.

Stimuli

Visual stimuli consisted of 3-second movie clips depicting the emotions happiness, disgust, fear or neutral. Unlike previous studies using dynamic displays (Kilts, Egan, Gideon, Ely, & Hoffman, 2003; LaBar, Crupain, Voyvodic, & McCarthy, 2003; Sato, Kochiyama, Yoshikawa, Naito, & Matsumura, 2004; Wicker et al., 2003), we had a range of facial expressions and more naturalistic specimens (no unecological morph technique was used). The happy condition consisted of spontaneous laughs by our actors, triggered by jokes. Fearful and disgusted expressions resulted from instructions to the actors to display prototypical, strong expressions of these emotions. The neutral condition consisted of an actor blowing up his/her cheeks. Actors, all Caucasian, were filmed from the shoulders up and were asked to express clearly the different emotions while limiting rigid head movements as much as possible. The movies were recorded digitally with a Sony DSR-PDX10P digital camcorder. Adobe Premier Pro Software was used to cut 3 s movie-clips starting with a neutral expression (slightly friendly) lasting for 0.5 s followed by the unfolding of the facial expression and ending on a strong facial expression. An extra control condition was used, displaying abstract pattern motions, composed of 0.5 s of a static oval shape patterned with vertical or horizontal stripes. Part of this pattern then started to swirl for 2.5 s. Twenty different actors

(10 males, 10 females) were filmed for all facial conditions. Each film was then rated on the content of basic emotions on a 7-point intensity scale (range 1–7) by an independent group of 15 subjects (according to methods used in Adolphs, Tranel, Damasio, & Damasio, 1994). On a separate 3-point scale (range 1–3), subjects rated how genuine the emotions looked. A score of 1 corresponded with a facial expression that looked “fake”, a score of 2 meant “doubtful genuineness” while a score of 3 corresponded with a “genuine looking” facial expression. Some of the actors were rated as displaying some emotions more intensely than other emotions, while other actors displayed their emotions more homogeneously. Out of the 20 actors, we selected five males and five females that showed the least differences between the intensity ratings of their target emotions. For this subset of actors, there were no significant differences between the intensity of the displayed target emotions (see Figure 2). On average, the chosen movie sets for the different conditions scored above 2 on the 3-point genuineness scale.

Procedure

The experiment was composed of three smaller experiments, each with a different instruction to the subjects. The observation and the discrimination tasks were conducted on the first scanning day, the imitation task on a second scanning day. Stimuli were presented using Presentation software (Neurobehavioral Systems, Inc., Albany, CA, USA).

Observation task. Subjects were instructed to pay careful attention to the different movie clips, without further explicit tasks. Stimuli were shown in a randomized event-related design with movies lasting 3 s and being separated by a random interval (average 6 s, range 4–8 s, hereafter written 6 ± 2 s) during which a white fixation cross was shown on a black background. The experiment was split into two functional runs lasting ~ 7.5 minutes. In each run, 5 out of the 10 movies of each condition were presented twice. After the functional runs, during the acquisition of an anatomical image, subjects had to perform a surprise memory task: They were shown 40 movies of single facial expressions, half of which had been shown to them during the functional runs. The 20 new movies were either movies of

the same actors performing different emotions than those used in this experiment or from different actors showing the same or different emotions as used in this experiment. Subjects had to indicate by means of a button press in a two-alternative forced-choice task if they had previously seen the movie.

Discrimination task. After the observation task, subjects received instructions for this second task. Subjects performed four functional runs (each lasting ~ 10 minutes) of a delayed match-to-sample task on emotions: movies were shown in pairs, subjects had to report by means of a button press whether the emotion of the first and second movie was the same or different. Only brain activity during presentation of the first stimulus in the pair was analyzed here, because it represents the brain activity during the deliberate extraction of the emotion from a facial expression, without the motor planning involved during the presentation of the second stimulus. Movie pairs were shown pseudo-randomly, 50% of the trials displayed the same emotion. Every movie was shown twice at the first position of movie pairs to enable comparisons between all tasks. Random intervals separated the two movies of a trial (4 ± 2 s) and two consecutive trials (6 ± 2 s). A red fixation cross was shown within movie pairs and between movie pairs the fixation cross was white. After this task, subjects were informed about the imitation task to follow a week later. Subjects were instructed to generate three personal scenarios that could help them to induce the tested emotions (e.g., sudden encounter with a spider, a dirty toilet, a good joke).

Imitation task (second scanning day). Participants had to watch a facial expression. After a random pause (4 ± 2 s) subjects had to (a) imitate the movements of the first movie during a 3-second period and (b) generate the corresponding emotion using the scenarios they had prepared ahead of time. In particular, subjects were instructed not simply to generate facial movements that are generic to the demonstrator’s emotion, but to imitate the particularities of that exemplar of the displayed emotion. Only the brain activity during the presentation of the movie was analyzed, to avoid contamination by motor execution. Data from this session thus represents brain activity while subjects explicitly pay attention to the motor aspects of a facial expression. Subjects were cued to start imitation by means of a change

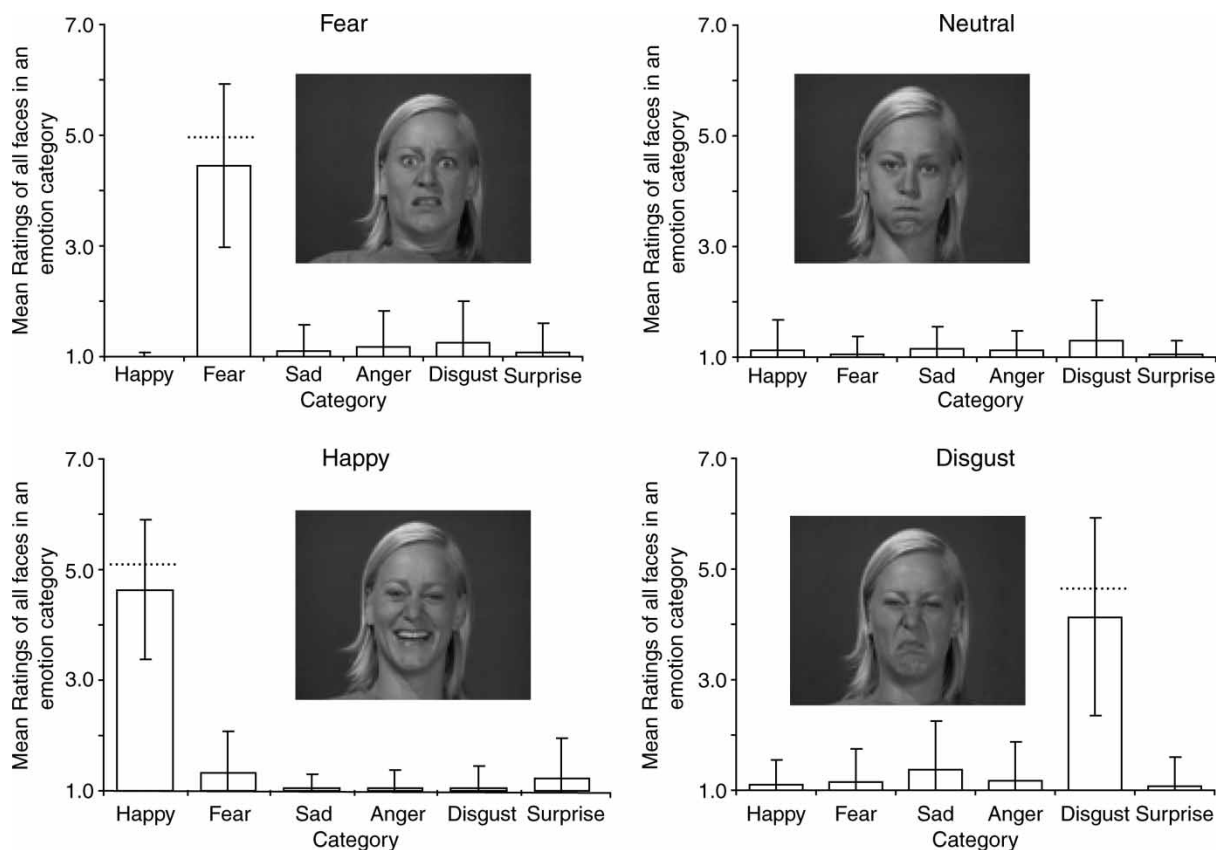


Figure 2. Ratings of emotional facial expressions on emotion words. Data are from an independent sample of 15 normal subjects. The photos are snapshots from one of the stimulus movies. The words in capitals above each graph refer to the stimulus category, those under each bar to the scale along which subjects had to rate the stimulus. The y-axis refers to reported intensity of the emotion, with 1 referring to “none” and 7 “very intense”, and error bars represent the standard-error of the mean (*SEM*) across 15 subjects. The second bar from the left on the top left plot thus refers, for example, to how much fear subjects saw in the fear stimuli. Dotted lines are mean ratings for the Ekman faces of the same category as adapted from Figure 2a in Adolphs et al. (1994). Note how these dotted lines fall within the error bars of the ratings of our stimuli.

in color of the fixation cross from red to green. Turning white of the same fixation cross was the signal to stop the imitation. Every movie-clip was shown twice.

For the purpose of analyses, the same number of trials of each condition were analyzed in all three tasks, namely 20 trials of each emotion. The discrimination task, due to the delayed matching to sample paradigm contained twice as many movies, but only the sample movies were analyzed. This allowed direct comparisons between the three sub-experiments.

Importantly, to avoid biasing mental processes during free viewing, subjects were held naive about the discrimination and imitation tasks ahead. Similarly, during the discrimination task, subjects did not yet know whether they had to perform an imitation task later. Tasks had to be

conducted in the fixed order: observation, discrimination, imitation for all subjects.

MRI data acquisition

Imaging data were acquired with a 3T Philips Intra MRI scanner (Philips, Best, The Netherlands). The standard 6-channel SENSE head coil was used to acquire whole brain echo-planar functional images (EPIs). Thirty-nine axial slices were acquired with the following parameters: TR 2000 ms; TE 30 ms; flip angle 90°; SENSE factor 2; field of view 224 mm; matrix 64 × 64; slice thickness 3.5 mm with no slice gap, yielding isotropic voxels of 3.5 × 3.5 × 3.5 mm in size. In addition, two anatomical images were acquired: one 3D-FFE to co-register and normalize functional data (TR = 25 ms, TE = 4.6 ms, flip angle = 30°,

FOV = 256 mm, matrix 256 × 256 mm, slice thickness 1.0 mm) and a high contrast 3D-T1TFE to trace the amygdalae (TR = 8.2 ms, TE = 3.7 ms, flip = 8.0°, FOV = 256 mm, matrix 256 × 256 mm, slice thickness 1.0 mm).

General data processing

A voxel-based analysis implemented in SPM2 (www.fil.ion.ucl.ac.uk/spm) was used first to analyze the fMRI data. Functional images were temporally adjusted for interleaved slice acquisition and then realigned to the first functional image of the first run. High quality T1 images were co-registered to the mean EPI image and segmented. Low-frequency signal drift was corrected by applying a high-pass temporal filter with a temporal cut-off of 250 s. Data preprocessing ended here for the analysis of signals in anatomically defined regions of interest (ROIs), here the left and right amygdala. For the whole-brain analyses, the co-registered grey matter segment was normalized onto the MNI grey matter template and the resulting normalization parameters applied to all EPI images. The functional data were spatially smoothed with a 6 mm isotropic Gaussian Kernel before the statistical analysis.

General linear model (GLM)

In all analyses below, a similar general linear model (GLM) random effect analysis was performed. For each subject, a GLM considering the time course of each condition, convoluted with the hemodynamic response was used to derive an average parameter estimate for each condition and subject. Parameter estimates could then be subtracted from each other to calculate contrast values. The contrast values from the 17 subjects were then compared against zero using one-sample *t*-tests to implement a random effect analysis (RFX). Resulting *p*-values are reported uncorrected for multiple comparisons. Input for this analysis could be the mean activity extracted from a region of interest (Brett, Anton, Valabregue, & Poline, 2002; <http://marsbar.sourceforge.net>) or the voxel by voxel activity of the entire brain using SPM2 (see below). Head movements were modeled as co-variates according to Friston, Williams, Howard, Frackowiak, and Turner (1996) for the imitation runs only.

Analyses of motor data alone. The data of the imitation task were modeled using separate predictors for the viewing of the movies, the retention interval and the production phase. Analysis relative to the viewing phase are reported below. The retention phase was not analyzed further in this manuscript. Data relative to the motor production phase were modeled with four predictors of interest—neutral (N), disgusted (D), fearful (F) and happy (H) imitation—and 24 motion covariates (see above) to remove confounding effects of head motion despite the fact that head motion never exceeded one voxel in this study.

In order to get a general view of activations during imitation, the sum of the parameter estimates for all four predictors was compared against zero at the second level and thresholded for display purposes at $p < .005$ (unless specified otherwise). To differentiate sub-regions more involved in producing emotional compared to neutral facial expressions, a contrast $D + F + H - 3N$ was thresholded at $p < .005$ and inclusively masked with $D + F + H + N$ at $p < .005$.

To investigate responses specific for particular emotions, two approaches were used. First the production of that emotion was contrasted against the production of the neutral emotion. To determine areas more involved in the production of one emotion compared to the other emotions, pairwise contrasts between the target emotion and the three remaining facial conditions were calculated. We required that all of these contrast needed to be significant at $p < .1$. In addition, the parameter estimate of the target emotion needed to be above zero at $p < .05$. Requiring that these four tests be significant results in a false positive rate under a global null hypothesis of $p_{\text{global}} < .1^3 \times .05 = .00005$ (see Friston, Penny, & Glaser, 2005, for a discussion of related issues). Unlike a traditional conjunction, this analysis has the advantage that each individual contrast needs to be above a certain threshold, making it more controllable. The logic behind requiring that the production of the particular emotion be above zero is to exclude regions from this analysis that do not respond to the target emotion but show only BOLD decreases to the other emotions.

Analyses of viewing data alone (observation, discrimination and viewing before imitation). In these analyses a GLM was generated in which 4 or 5 predictors of interest were identified per task

(four facial conditions and an additional pattern condition for the observation and discrimination task). For the observation task, no other predictors were modeled. For the discrimination task, 10 additional predictors were modeled, which were not analyzed here (the retention intervals and the second stimuli for all five conditions). For the imitation task, only the four predictors relative to the viewing of the stimuli were analyzed here (with the motor execution predictors analyzed as discussed in the motor section before). To restrict ourselves to mirror activations, results of the viewing phases were masked inclusively by the motor production maps obtained from the analyses described above.

Analyses of mirror activities combining all facial conditions. To investigate mirror activations, we combined data from viewing a certain stimulus with data obtained while subjects produced similar facial expressions. The two sets of data were combined using logical “AND” analysis, identical to inclusive masking (Keysers et al., 2004; Wicker et al., 2003). For viewing, we analyzed either the “viewing of all facial expressions – rest” to study the general MNS, the “viewing of all faces – pattern” to search for biological motion specificity in the MNS or the “viewing of emotional faces – neutral faces” to identify the emotional MNS. For motor production, we compared “production of all facial expressions – rest” to study the general and biological motion specific MNS or the “production of emotional faces – neutral faces” to study the emotional MNS. Moderate thresholds of both (viewing and production) group t -maps ($p < .005$) were combined, resulting in an overall false positive under a global null hypothesis of $p < .000025$. Results were then displayed using a spatial threshold of 20 voxels ($k = 20$).

To study task effects in the MNS, the above-mentioned analyses were performed for each vision task individually (observation, discrimination and viewing before imitation) and consecutively compared as a paired t -test to the parameter estimates under the different instructions. The emotional MNS was studied by combining the viewing of facial expressions during both the observation and discrimination tasks, therefore increasing statistical power.

Analyses of mirror activities of individual emotions. Mirror activations for specific emotions were studied in two ways. The first used a classical

approach by searching for overlap between the group t -map of viewing of that emotion minus the neutral condition (e.g., fear–neutral) and the group t -map of imitation of that facial emotion minus neutral (e.g., fear–neutral). Thresholds were used as described above ($p < .005$, $k = 20$).

For mirror activations for specific emotions we used a similar approach as the one described above to analyze activations related to the *production* of specific emotions, differing only by increasing the number of statistical tests that were combined: here we required that comparing the target emotion (including neutral) against the other facial conditions needed to be significant in each case both during viewing and during production, and that both during viewing and production the target emotion by itself exceeded zero, i.e., for fear, we tested F–N, F–H, F–D for viewing and for execution at $p < .1$ and F by itself for execution and viewing at .05. Combining these 8 tests leads to a false positive rate under the global null of $p < .025 \times 10^{-8}$.

ROI analysis of the amygdala. A previous study by Carr et al. (2003) found activation overlap within the right amygdala during both emotional facial expression imitation and observation. In a previous study, the role of the amygdalae during viewing was studied using a voxel-wise analysis and an ROI approach with MarsBar and individually defined amygdalae (see Van der Gaag et al., 2007; Appendix 1). During viewing, we could not find a difference between any emotional facial and neutral facial motion observation applying the two mentioned methods. Therefore, to further clarify the role of the amygdalae during imitation, the ROI approach was applied here as well.

RESULTS

We will first discuss the results of the motor execution phase of the imitation task in order to identify voxels in the brain involved in the production of facial expressions (section a). Resulting maps will be used as masks to locate mirror circuits during the different viewing conditions (section b). The rationale behind that procedure is that “mirror-voxels” have to be active both during the production and the observation of facial expressions. In section c, we will test the specificity for biological motion within the MNS. Section d will investigate

whether certain voxels within the MNS might be more involved in particular emotions, including the involvement of the amygdala and insula.

Behavioral data. Behavioral results of three subjects could not be analyzed due to malfunctioning of the computer that recorded key-presses during scanning sessions. Behavioral data presented are therefore based on the analysis of the remaining 14 subjects. Data from all 17 subjects were kept for the fMRI analysis.

Surprise memory task. Subjects showed a good performance on this task: on average 93% of the new stimuli were correctly identified while 84% of the familiar movie clips were identified as such. All subjects scored >70%, calculated as (correct rejection+hits)/number of trials, on the memory task, suggesting that subjects paid attention to our stimuli during the observation task.

Discrimination task. On average, 92% of the “same emotion” trials, and 97% of the “different emotion” trials were correctly identified, respectively. All subjects scored >80% on this task, justifying the conclusion that all our subjects paid attention during the delayed match-to-sample-task.

No performance data were acquired during the imitation task, although gross motor movements of the subjects were monitored by an independent observer with an infra-red camera installed in the MRI environment. Facial movements during the appropriate moment of the imitation task were confirmed for all our subjects.

(a) The neural circuit involved in facial imitation

First, combining all motor execution conditions (emotional and neutral facial expressions) we found a circuit very comparable to that reported in previous studies (Carr et al., 2003; Dapretto et al., 2006; Hennenlotter et al., 2005; Leslie et al., 2004) composed of primary motor, pre/supplementary motor, somatosensory, posterior parietal, and visual areas, in particular STS/MTG (Appendices 2 and 3). The premotor activations extended into BA 45. In addition, we found sectors of the insula, hypothalamus, basal ganglia and cerebellum to be involved. Comparing the execution of the emotional with that of the neutral facial expressions revealed that in the vast majority of

the areas involved in the production of facial expressions, sub-areas were more active during the production of the emotional facial expressions. (A detailed description of the areas is reported in Appendices 4 and 5.)

While the activations found in frontal and parietal areas in our data can be attributed to the motor execution and somatosensory consequences of these movements, activations in visual areas may have been related to either the generated emotional scripts, the working memory trace of the facial stimuli subjects had to imitate or to the generation of a visual image of what the facial expression they are currently producing would look like in order to match the target facial expression (Iacoboni et al., 2001; Keysers & Perrett, 2004).

These motor execution maps will be used in the remainder of the manuscript to restrict the analysis of visual responses to areas also involved in motor production in order to identify mirror regions. The potential influence of the visual stimuli inherent to our imitation task need to be kept in mind when interpreting the results obtained from masking visual activations with the motor production maps, particularly in areas known to have prominent visual activations (e.g., MTG/STS).

(b) The MNS of facial expressions and its task effects

The overlap between viewing during the observation of dynamic facial expressions (without an explicit task) and facial expression production included areas classically considered to be the MNS, bilateral inferior frontal gyrus and rostral sectors of the posterior parietal cortex (Figure 3A; Appendix 6). In addition, overlaps were found in SMA, SI and SII, the insula, amygdala, hippocampus, cerebellum, and a number of visual areas (Area 17/18, fusiform gyrus, MTG). In essence, the circuit we found is similar to that of Carr et al. (2003).

Activations in SI and SII have been reported before in action observation (Avikainen, Forss, & Hari, 2002) and, in the case of facial perception, might be important for emotion understanding (Adolphs et al., 2000). The study by Carr et al. (2003) only showed SI activation during imitation and not during observation, however, their stimuli were static in comparison with our dynamic movies. Of the reported limbic regions, insula

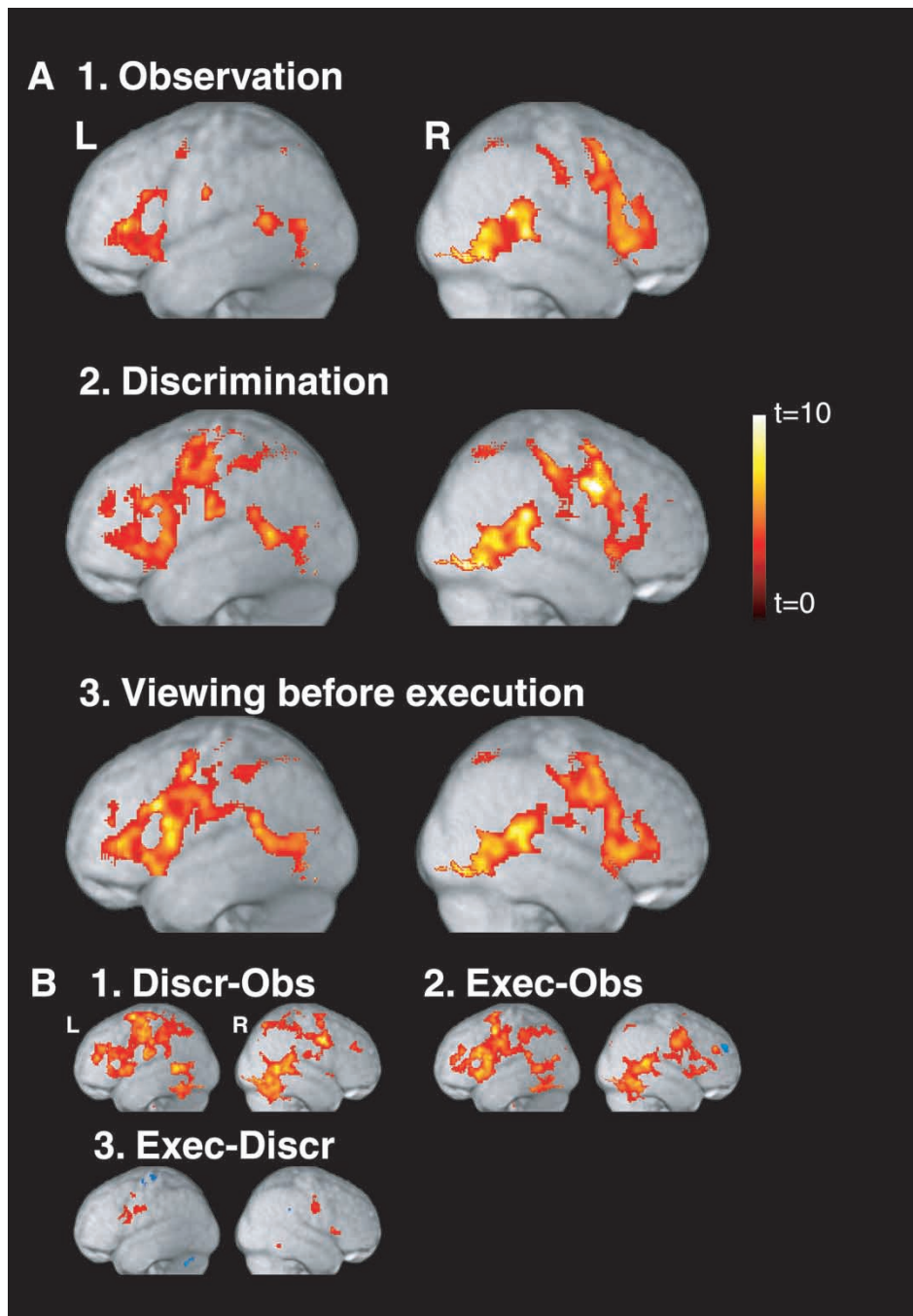


Figure 3. MNS analyses during the different task conditions. (A) shows those brain regions that are active during facial expression viewing, all four facial conditions combined – rest, $t(16) > 2.92$, $p < .005$, $k = 20$, inclusively masked with facial expression execution. The same analysis was performed with passive observation (1), discrimination (2) and viewing-before-imitation (3) as viewing conditions. (B) shows brain regions that significantly differentiate between facial viewing tasks, matched pair t -test, $t(16) > 2.92$, $p < .005$, $k = 20$, inclusively masked with facial expression production, all four facial conditions – rest, $t(16) > 2.92$, $p < .005$. The following pairwise comparisons were performed: discrimination contrasted against observation (1), viewing-before-imitation contrasted against observation (2), and viewing-before-imitation contrasted against discrimination (3). Inclusive masking at $p < .005$ of a contrast thresholded at $p < .005^2 \geq p < .000025$. Results are overlaid on an averaged T1-weighted 3D render of the 17 subjects. (See Appendices 6 & 7 for coordinates of local maxima.)

involvement in the processing of facial emotions using a mirror-paradigm has also been observed before (Carr et al., 2003; Hennenlotter et al., 2005; Wicker et al., 2003), but only the study by Carr et al. (2003) reported amygdala involvement. The amygdala involvement during facial expression imitation and its mirror neuron capacities will be discussed further in section d. Overlap in visual areas is unlikely to be caused by the presence of mirror neurons with true motor properties in these regions. As discussed above, overlaps are more likely to be due to visual components of the imitation task.

With this analysis we have shown that inferior frontal regions become active when subjects view unfolding facial expressions, even if they are unaware of an upcoming imitation task. This is important, as it shows that premotor results of previous studies (Carr et al., 2003; Hennenlotter et al., 2005; Leslie et al., 2004) can not entirely be explained by anticipated motor requirements of the task.

In general, our two active tasks (discrimination and imitation) lead to stronger and more extensive brain activations. From the discrimination task (delayed match-to-sample), only the sample facial expression was analyzed. Defining the mirror neuron circuit based on the viewing phase of the discrimination task instead of the observation task, reveals a number of additional brain regions: the bilateral middle frontal gyrus, putamen, inferior parietal cortex, middle cingulate gyrus and the left primary motor area (Figure 3A; Appendix 6). From the imitation task, only the vision of facial expression movies were analyzed here, the imitation episode was temporally separated and analyzed in section a. Results based on the viewing part of imitation resembled those during the discrimination task.

Comparing the different tasks directly (Figure 3B; Appendix 7), we found that the viewing phase of discrimination and imitation resulted in significantly stronger brain activations than the more passive observation task demonstrating task influence on the mirror system. Increased brain activation during the active tasks could be related to increased visual attention or to working memory (Druzgal & D'Esposito, 2003; Haxby, Petit, Ungerleider, & Courtney, 2000). Premotor and parietal augmentations may additionally be linked to motor requirements of the response requested from the subjects (button press/facial expression production; Grezes, Costes, & Decety, 1999; Grezes

& Decety, 2001). Only the anterior right superior frontal gyrus was more involved in observation compared to imitation. No brain area was more active during the observation task than during the discrimination task. While our data thus suggest that the activity of the MNS can be modulated by attentional factors, the origin of this modulation is likely to lie outside of the MNS (e.g., see Corbetta & Shulman, 2002).

Comparing the viewing phase during the discrimination and imitation tasks directly revealed differences in areas related to the motor system, premotor, primary motor, cerebellum, putamen and globus pallidus (Figure 3B; Appendix 7). Interestingly, the primary motor differences were compatible with the differences in task requirement: the discrimination task requiring the pressing of a button with the right hand determined stronger activations in a dorsal sector of the contralateral M1, while the imitation task requiring facial movements determined larger activations in a ventral sector of bilateral M1 known to relate to facial movements (Carr et al., 2003; Dapretto et al., 2006; Hennenlotter et al., 2005; Leslie et al., 2004). This finding suggests that a readiness to provide motor output can bias activation in paradigms investigating mirror activity, and advocates the use of paradigms not requiring motor output in order to get a "pure" estimate of mirror activity. Despite these task differences, the overall pattern of areas defined as "mirror" in all three tasks (Figure 3A) is reassuringly similar.

In summary, the classical MNS and some affective regions like the insula and amygdala resonate during the observation of facial expressions. This circuit becomes spontaneously active when we watch facial expressions, even when subjects are unaware of future imitation tasks. The addition of cognitive tasks to the observation process that have to result in a motor output increases not only the amplitude of activated brain regions, but also the extent of the activated neural circuit. Paying attention to the muscular movements itself during the viewing episode of the imitation task or adding meaning to these muscular movements during the discrimination task influences the circuit similarly.

(c) Specificity in the MNS for biological motion

Figure 4 shows the results of the brain activation during the viewing of faces compared with that

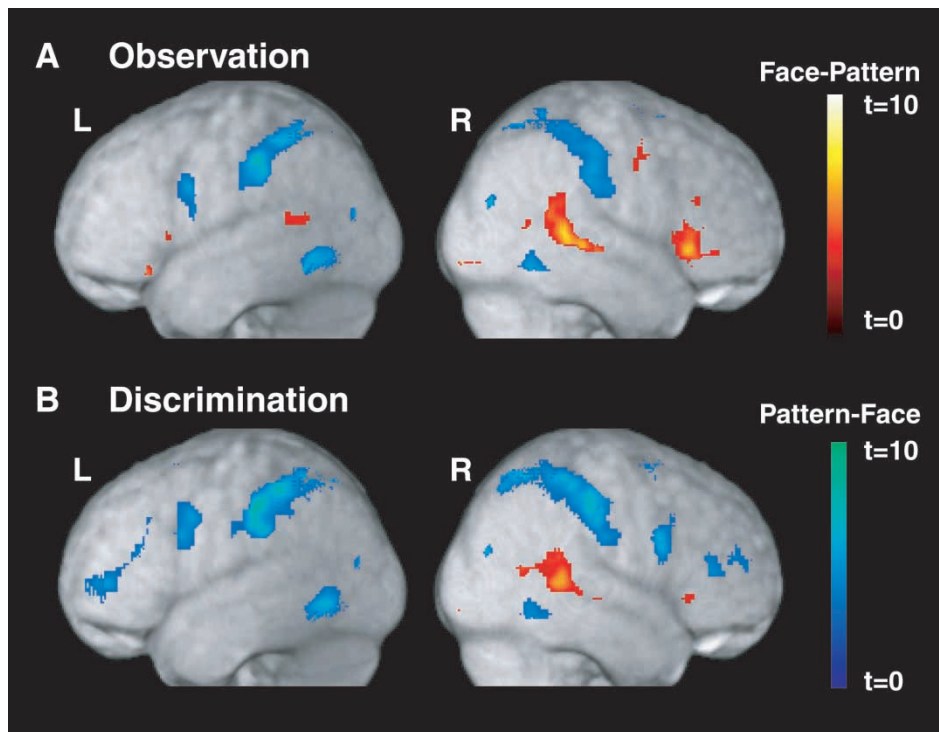


Figure 4. Signal increases in the MNS for the contrast dynamic faces – dynamic patterns during the passive observation (A) and the discrimination (B) task. Warm colors show brain regions that prefer the observation of dynamic faces over dynamic patterns, all four facial conditions combined-patterns, matched pair t -test, $t(16) > 2.92$, $p < .005$, $k = 20$, while cold colors represent brain regions that prefer the observation of dynamic patterns over facial expressions, matched pair t -test, $t(16) > 2.92$, $p < .005$, $k = 20$. All regions shown are also inclusively masked with facial expression production, all four facial conditions – rest, $t(16) > 2.92$, $p < .005$. The same false positive rate as explained in Figure 3 applies. (See Appendix 8 for coordinates of local maxima.)

during the observation of patterns, within the MNS described in section b. The bilateral ventral inferior frontal gyrus, bilateral STS/MTG, bilateral amygdala, SMA, the right lateral fusiform gyrus and the bilateral cerebellum (Appendix 8) all responded significantly more during the viewing of facial movements compared to pattern movements (in addition to being involved in the production of facial movements). This is in agreement with studies that compared static faces and patterns (Gorno-Tempini et al., 2001; Kesler-West et al., 2001). This biologically specific MNS is substantially more restricted than the MNS defined under section b. Interestingly, the parietal nodes of the classical MNS are activated more by moving patterns than faces while parts of the MTG and inferior frontal gyrus are more selective for faces. This is in agreement with a series of fMRI studies by Schubotz (Schubotz & von Cramon, 2001, 2002, 2004), showing activation of the ventral premotor cortex and posterior parietal regions in abstract pattern sequence processing. In a study containing biological motion and pattern sequence observation, only

the pattern condition activated the parietal regions (Schubotz & von Cramon, 2004). Besides a role in action observation and execution (Fogassi & Luppino, 2005), the posterior parietal area in monkeys has been shown to be involved in visuomotor transformations and space representations (Fogassi et al., 2005). Recent studies suggest a role of parietal areas in object recognition (Fogassi et al., 2005; Janssen, Vogels, Liu, & Orban, 2001), and widespread connections with inferior temporal regions (Luppino, Murata, Belmalih, Calzavara, & Rozzi, 2004) could provide the detailed visual input necessary for this function. Indeed, we also find higher inferior temporal activations during our pattern condition than during our face conditions. Alternatively, the identification of unfamiliar pattern movements might simply require more attentional resources, and this attentional effect might overshadow the significant parietal activations found during facial observation located in section b. Pattern processing might require more parietal involvement because pattern processing is less holistic than face processing and may thus require more

explicit processing of the spatial relationship between the elements composing the moving pattern. During facial processing, more activation was observed in areas known to specialize in the processing of faces, the fusiform gyrus and MTG/STS (Kanwisher, McDermott, & Chun, 1997; Perrett, Rolls, & Caan, 1982).

Premotor mirror regions identified in section b were much reduced if contrasted with pattern motion. Of Broca's area and its right-sided homologue, only some ventral and anterior parts survived a direct contrast. This is in accordance with data by Schubotz and von Cramon (2004), showing comparable frontal activations during observation of biological hand movements compared with the observation of pattern sequences. Regions of premotor cortex commonly activated during facial expression and pattern observation might reflect general sequence processing qualities (Sakreida, Schubotz, Wolfensteller, & von Cramon, 2005). Because our ventral inferior frontal gyrus activations are bilateral with stronger activations on the right side, it is unlikely that they are due to silent naming of, for example, the facial expressions (Grezes & Decety, 2001).

From the present data, BA 44/45 could thus contain neurons that would selectively map the sight of facial movements onto motor programs involved in facial expressions. Due to the limitations of fMRI, this conclusion can only be tentative. Single-cell recordings in primates, however, have demonstrated the existence of neurons responding to facial expressions more than to other stimuli (O Scalaidhe, Wilson, & Goldman-Rakic, 1997) in an area of the inferior frontal cortex that could correspond to BA 44/45 (Petrides, Cadoret, & Mackey, 2005). The same area has been shown to contain neurons selectively involved in orofacial actions. Unfortunately, whether the same neurons in this area respond both to the observation and execution of facial expressions has not yet been tested.

As the only form of biological movement in this experiment was of facial nature, the stronger responses in BA 44/45 could reflect specificity for *facial* movements or specificity for *biological* movements. A number of studies have found ventral premotor areas to respond more strongly to face compared to hand actions (Buccino et al., 2001; Sakreida et al., 2005; Wheaton, Thompson, Syngeniotis, Abbott, & Puce, 2004) supporting the idea that BA 44/45, although not exclusively devoted to the face, may indeed be particularly

involved with the execution and observation of facial actions.

A similar pattern of results was observed when facial and pattern processing was analyzed during the discrimination task, although premotor activations to faces were less pronounced during discrimination. Habituation due to the fact that the same stimuli were used in both tasks and that discrimination always occurred after observation may explain this difference. In addition, the requirement for motor output during discrimination even for the patterns may have influenced these results.

In sum, this analysis shows that only limited premotor regions show biological motion specificity. Anterior portions of the ventral premotor cortex might be the site for the direct matching of observed facial expressions onto the motor representation of facial expressions in the observer. More dorsal and posterior premotor regions might be involved in sequence processing, be it of biological motion or not. Pre-SMA and the cerebellum showed areas of biological selectivity.

(d) Emotion specificity in the MNS

First, we searched for an overlap in the observation and execution of facial expressions. Therefore, a similar contrast comparing the emotional facial conditions with the neutral condition was performed both during viewing and production tasks. The bilateral insula/frontal operculum (IFO; including bilateral BA 44 and right BA 45), the right anterior STS and the pre-SMA (Figure 5; Appendix 9) were involved in both tasks. All these regions are biologically specific as well, as they are also activated in the contrast described under section c. Previous studies found increased ventral premotor activations due to observation (e.g., Gorno-Tempini et al., 2001; Kesler-West et al., 2001; Sprengelmeyer, Rausch, Eysel, & Przuntek, 1998), volitional and spontaneous production (Wild et al., 2006) or observation and imitation (e.g., Carr et al., 2003) of facial expressions. The insula was reported to be active in both facial expression observation and execution in two studies, one that combined several emotions in their analysis (Carr et al., 2003) and one that only studied smiling facial expressions (Hennenlotter et al., 2005). In both studies the neutral facial condition did not contain implicit or explicit movements. We therefore show for the first time that emotional facial expression

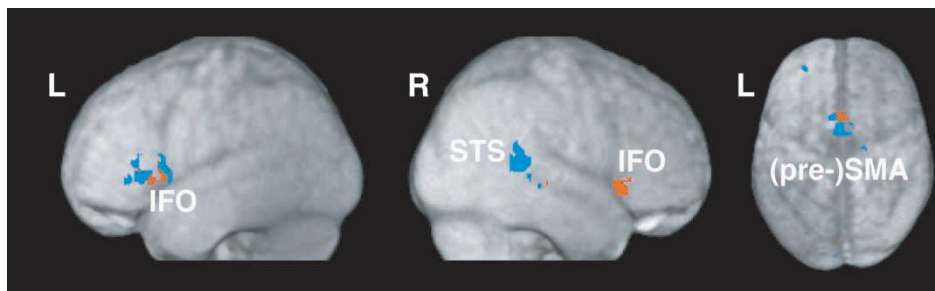


Figure 5. Signal increases for the viewing of emotional facial expressions minus neutral facial expressions, after combining the observation and discrimination task, average of three emotional facial conditions – neutral facial condition, $t(16) > 2.92$, $p < .005$, $k = 20$. Blue regions are areas that do not differentiate between the execution of emotional and neutral facial expressions, average of three emotional facial conditions combined – neutral facial condition, $t(16) > 2.92$, $p < .005$, $k = 20$, despite the inherent difference during viewing, while orange areas differentiate between the execution of emotional and neutral facial expressions, average of three emotional facial conditions combined – neutral facial condition, $t(16) > 2.92$, $p < .005$, $k = 20$, in addition to the viewing difference (congruent mapping). The same false positive rate as explained in Figure 3 applies. (See Appendix 9 for coordinates of local maxima.) L=left hemisphere; R=right hemisphere; IFO=insula/frontal operculum; STS=superior temporal sulcus; SMA=supplementary motor area.

observation and execution overlaps in bilateral IFO, when both the neutral and emotional facial expressions contained facial movements. Motor programs for emotional facial expressions located in the ventral inferior frontal cortex of the observer might resonate when emotional facial expressions are witnessed. This effect might simply be a reflection of the increased complexity of the emotional facial expressions, as the movements in the neutral condition were only limited to the lower regions of the face. The increased complexity entails at the same time an (emotional) intention (see Figure 2), which has recently been shown to increase the activation within inferior frontal cortex (Iacoboni et al., 2005).

Looking at the reverse contrast, neutral–emotional, we could locate brain regions that are significantly more active during both the viewing and execution of the neutral condition over emotional facial expressions. Bilateral SI and right SII (Appendix 9) are significantly more active during the viewing and execution of neutral facial expressions compared with emotional facial expressions. Although we cannot exclude the possibility that subjects overtly blew up their cheeks during our viewing condition, located brain regions are very similar as found by a study by Blakemore, Bristow, Bird, and Frith (2005) that analyzed the overlaps between the viewing and experiencing of touching the face.

In conclusion, there seems to exist a dissociation between the viewing and experiencing of neutral facial movements like blowing up the cheeks and the viewing and experiencing of

emotional facial movements: blowing up the cheeks activates relatively more somatosensory regions (SI and SII), while emotional facial movements activate the IFO relatively more. This makes sense, as emotional facial expressions are more related to interoceptive representations of emotions supported by the insula (Craig, 2002; Damasio et al., 2000), while blowing up the cheeks may activate relatively more extero- and proprioceptive pathways, which eventually terminate in parietal somatosensory cortex like SI and SII (Craig, 2002).

Second, we tested whether we could find evidence of mirror neuron systems for specific facial conditions. We will focus our analyses on the IFO and amygdala as previous studies have shown that the insula is important for disgust recognition and experiencing and the amygdala might be important for fear recognition and experiencing (Calder et al., 2001; Keysers & Gazzola, 2006; however see Adolphs & Spezio, 2006; Van der Gaag et al., 2007). Moreover, these two regions were found to be active during both the observation and production of a combined analysis of six basic facial expressions (Carr et al., 2003). We showed above that only the (bilateral) IFO is involved in a direct matching analysis of emotional facial expressions, in which we combined all emotions to compare it with neutral. The amygdala was not activated in this general analysis because, unlike Carr et al. (2003), we used a more stringent analysis, contrasting emotional facial expressions not against a fixation condition but against a neutral facial expression (Van der Gaag et al., 2007). We also performed

analyses on the somatosensory cortex as we located this region bilaterally in our direct matching analysis contrasting neutral facial expressions with emotional facial expressions. The somatosensory cortex has been attributed to have an important role in the recognition of facial expressions (Adolphs, 2002; Adolphs et al., 2000; Damasio et al., 2000).

To look into the question of facial condition specificity, we extracted the signal from the regions found in the general analysis (Figure 5; Appendix 9) for each condition individually (this was not possible for the amygdala as this structure was not activated in the general analysis) and tested the regions on condition specificity. A two-way analysis of variance (ANOVA) was performed with Task (viewing, execution) and Facial Condition (neutral, disgust, fear, happy) as predictor variables. We label areas as “specific” for a target facial condition if the target condition is significantly more active than all the other facial conditions in this analysis.

In the right IFO (Figure 6A), there was a significant main effect of task, $F(1, 16) = 11.1$, $p < .004$, with higher parameter estimates during execution. There was also a significant main effect of emotion, $F(3, 48) = 15.0$, $p < .001$. There was no significant interaction on parameter estimates, $F(3, 48) = 2.2$, $p > .102$, between task and condition. Simple contrasts comparing disgust with the remaining facial conditions (*a priori* hypothesis) showed that the parameter estimates during neutral, $F(1, 16) = 39.4$, $p < .001$, differed significantly from disgust, however, fear and happy did not significantly differ from disgust ($p > .25$), in accordance with the finding of Jabbi et al. (2007).

In the left IFO (Appendix 10A), the same pattern was true, with significant main effects of task, $F(1, 16) = 4.94$, $p < .04$, and emotion, $F(1.63, 26) = 15.8$, $p < .001$ (Greenhouse–Geisser corrected). There was no significant interaction on parameter estimates, $F(3, 48) = 1.54$, $p > .22$. Simple contrasts comparing disgust with the remaining facial conditions showed again that parameter estimates during neutral, $F(1, 16) = 47.3$, $p < .001$, differed significantly from disgust, however, fear and happy did not significantly differ from disgust ($p > .15$). The SMA and STS (as defined in Appendix 9) also failed to show specificity for any of the emotions used (Appendix 10A).

Fear specificity in the amygdala was tested by means of extracting the signal from *anatomically* defined amygdala (see materials and methods).

During the different viewing conditions, the amygdala was not specific for fear or any of the other facial conditions, as reported elsewhere (Van der Gaag et al., 2007). During facial expression production, we performed a two-way analysis of variance (ANOVA) with Hemisphere (left, right) and Facial Condition (neutral, disgust, fear, happy) as predictor variables. There was a significant main effect of facial condition, $F(1, 16) = 7.7$, $p < .011$, however no significant main effect of hemisphere, $F(3, 48) = 5.9$, $p > .45$, and no significant interaction, $F(3, 48) = 15.0$, $p > .45$. The left amygdala was less active during fear compared to all other emotions (Figure 6C), however this difference was significant only compared to happiness ($p < .05$) explored by Newman–Keuls post hoc analyses. In the right amygdala, the same trend was true, fear significantly lower than happiness ($p < .0005$) with significantly less activation during fear against neutral ($p < .005$). In conclusion, also during the different imitation conditions, the amygdala was not specific for fear or any of the other facial conditions. A voxel-wise analysis of the IFO and amygdala led to similar results (Appendix 9: no IFO in the disgust specificity analysis and no amygdala in the fear specificity analysis).

In the right SI (Appendix 10B), there was a significant main effect of task, $F(1, 16) = 6.9$, $p < .02$, with higher parameter estimates during execution. There was also a significant main effect of facial condition, $F(3, 48) = 9.8$, $p < .001$. There was no significant interaction, $F(3, 48) = 0.01$, $p > .99$, between task and condition. Simple contrasts comparing neutral with the remaining facial conditions showed that neutral differed significantly from all the other facial conditions ($p < .01$).

In the left SI, the same pattern was true (Appendix 10B), with a significant main effects of task, $F(1, 16) = 10.9$, $p < .005$, and facial condition, $F(3, 48) = 16.7$, $p < .001$. There was no significant interaction, $F(3, 48) = 1.0$, $p > .4$. Simple contrasts comparing neutral with the remaining facial conditions showed again that the neutral condition differed significantly from the emotional conditions ($p < .005$).

In the right SII (Figure 6B), there was a significant main effect of task, $F(1, 16) = 19.2$, $p < .001$, and facial condition, $F(3, 48) = 15.4$, $p < .001$, without a significant interaction, $F(3, 48) = 1.6$, $p > .1$, between task and condition. Simple contrasts comparing neutral with the remaining facial conditions showed that the

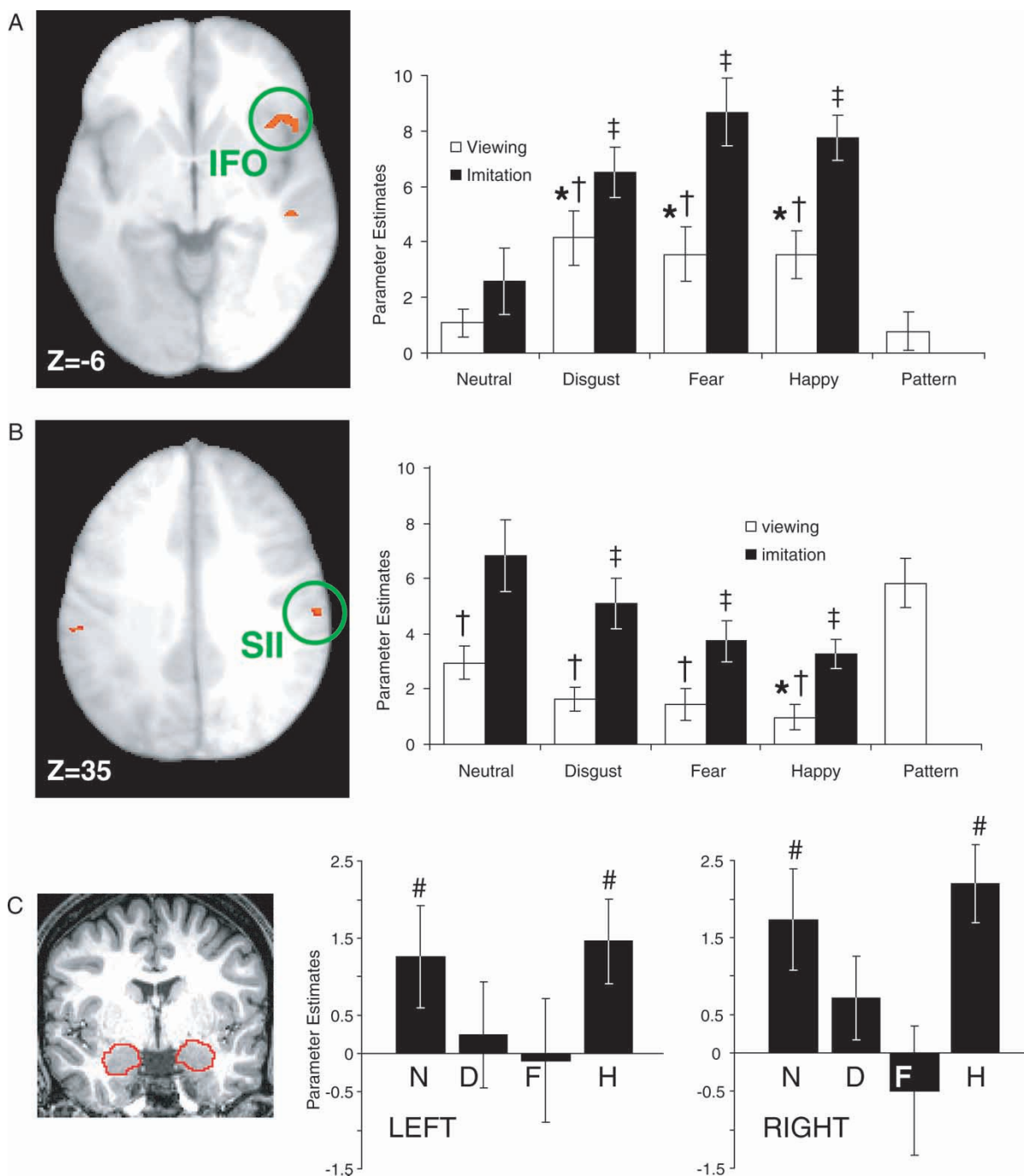


Figure 6. (See facing page for caption.)

neutral condition differed significantly from all facial emotional conditions ($p < .005$).

In summary, the IFO seems to be a region that is more involved in the observation and production of emotional facial expressions compared with neutral facial expressions, which is in agreement with previous findings (e.g., Carr et al., 2003). The insula might be a region with emo-

tional mirror neuron properties, although we did not find evidence for a disgust specificity in the insula (like Damasio et al., 2000; Morris et al., 1998; Phan et al., 2002; Schienle et al., 2002). As has been suggested previously (Carr et al., 2003), the insula might be a relay station between the classical MNS and limbic regions like the amygdala important for emotional processing. We

found the amygdala to be activated during facial expression observation and production (see section b), however, activations during viewing and production of *emotional* facial expressions were not significantly higher than during *neutral* facial expressions when both neutral and emotional facial expressions contain facial movements. Specificity of the amygdala in fear recognition and production could not be established. We therefore did not find evidence for the existence of an *emotional* MNS in the amygdala. This fits with more recent data showing that the amygdala is not an essential site for fear recognition (Adolphs et al., 2005; Adolphs & Spezio, 2006) and not essential for the volitional production of facial expressions including fear (Anderson & Phelps, 2000).

In contrast, bilateral SI and right SII show higher activations for blowing up the cheeks (our neutral condition) than for our emotional facial expressions.

Finally, we performed a general and preliminary search for regions specifically involved in the observation and production of particular facial movements (Appendices 9, 11 & 12). For the neutral facial condition, specific overlaps between observation and execution were found in right SI, bilateral SII, and premotor cortex, which fits with our previous analysis contrasting neutral with emotional facial expressions during both observation and execution (see above). For disgust, the left putamen, the left lingual gyrus, the right fusiform gyrus and occipital regions showed mirror properties. Overlap in observation and production of fearful facial expressions were found in bilateral inferior frontal cortex, right middle frontal gyrus, right premotor cortex and

left middle temporal gyrus. Only two regions were happy specific, which were the right superior medial gyrus and right superior temporal gyrus.

Summarizing the previous sections, only minor differences in the MNS were found between facial expressions. Comparing emotional facial expressions with blowing up the cheeks there is, however, a clear difference. Emotional facial expressions selectively activate the IFO region more in both viewing and execution, supporting the occurrence of motor and emotional simulation during the viewing of emotional facial expressions. During the viewing of our neutral expression we found evidence for increased somatosensory simulation compared with our emotional conditions. We hypothesize that in combining simulation at motor, somatosensory and limbic levels one really gains insight into what is happening in other people.

Several limitations apply to this part of the study: the displayed actors on the movies were unfamiliar to the subjects, the context in which the actors showed the facial expressions was absent in addition to the absence of a real interaction between subjects and actors when using film clips. As a result, the viewing conditions of the emotions displayed were of limited self-relevance to the subjects being scanned. Activations of our viewing tasks might therefore be more related to physical aspects of the stimuli used than to emotional processing. Second, the cognitive generation of an emotion is likely to be different from a spontaneous emotional experience in daily life. Moreover, a spontaneous emotional facial expression might be processed through a partly different neural circuit than the volitional production of one

Figure 6 (opposite). Contrast values of the different viewing and execution conditions from several ROIs. Contrast values from the different ROIs were extracted from individual subjects using the MarsBar toolbox (see material and methods). (A) Left: Right IFO ROI resulting from the congruent mapping analysis of the emotional facial expression minus neutral facial expression contrast, as depicted in Figure 5 and listed in Appendix 9; Right: Contrast values for the different stimuli during both viewing, combining observation and discrimination (white bars) and execution (black bars) from our IFO ROI. Error bars represent the *SEM*. The significant main effect of condition (see results) was further explored using Newman-Keuls post hoc comparisons: emotional facial conditions that significantly differed from the neutral condition during *viewing* ($p < .05$) are marked with an asterisk (*), facial conditions that significantly differed from the pattern condition during *viewing* ($p < .05$) are marked with a dagger (†), emotional facial conditions that significantly differed from the neutral condition during *execution* ($p < .05$) are marked with a double dagger (‡). Comparisons of the disgust condition with the remaining facial conditions within the IFO (*a priori* hypothesis) is discussed further in the text. (B) Left: Right SII ROI resulting from the congruent mapping analysis of the neutral facial expression minus emotional facial expression contrast as described in Appendix 9; Right: contrast values taken from the SII ROI during the different conditions. The same explanation for the graph and the symbols apply as described under (A). (C) Results from the anatomically defined amygdala analysis. Left: example tracing of left and right amygdala shown on one slice; Right: Contrast values for the different *execution* conditions for the left and right amygdalae. Conditions marked with a hash (#) produced activations that significantly differed from zero according to a one-tailed *t*-test ($p < .05$). Emotional facial conditions were never significantly larger than the neutral condition. The fear specificity analysis (*a priori* hypothesis) is described further in the text. IFO = insula/frontal operculum; SII = secondary somatosensory cortex; N = neutral facial condition; D = disgust; F = fear; H = happy.

(Hopf, Muller-Forell, & Hopf, 1992; Iwase et al., 2002; Wild et al., 2006). These drawbacks might explain the limited limbic system involvement in our emotional mirror system analyses. Our analysis has therefore to be regarded as preliminary, located “mirror areas” have to be replicated for the different emotions but can be useful in generating hypotheses.

GENERAL DISCUSSION

Mirroring of facial expressions has recently generated a lot of attention (Adolphs, 2006; Carr et al., 2003; Dapretto et al., 2006; Goldman & Sripada, 2005), not least because the MNS is hypothesized to be the neurological basis of fundamental human capacities such as empathy (Gallese et al., 2004). Encouraging evidence has been reported that the MNS is indeed involved in the observation of facial expressions in humans, although the exact nature of this MNS involvement remains rather sketchy. Moreover, important evidence from comparative single-cell studies in monkeys on the mirroring of facial expressions is still lacking.

Using dynamic displays of both emotional and neutral facial expressions, we found the bilateral inferior frontal gyrus (including sections of BA 44 and BA 45) and inferior parietal cortex to be involved in both the observation and execution of facial expressions. In addition to these “classical” MNS sites, we found a number of other regions to be involved in the observation and execution of facial expressions: STS–MTG, insula, amygdala (pre-)SMA and somatosensory cortex (SI and SII), hereafter called “extended” MNS. These findings replicate previous studies on this topic (Carr et al., 2003; Dapretto et al., 2006; Leslie et al., 2004). We studied the extent to which activations in the “classical” and “extended” MNS could depend on specific task instructions given to the subjects during the viewing of the facial conditions. Task effects within the “classical” and “extended” MNS could be established, although the different instructions essentially activated the same circuit. A passive observation task spontaneously activated the “classical” and “extended” MNS, even when subjects were unaware of an upcoming execution task. This finding is important, as several previous studies that reported activations within the MNS during facial expression observation all used paradigms in which observation and execution were intermixed

conditions (Carr et al., 2003; Dapretto et al., 2006). Similarly, in other studies subjects knew during the observation of facial expressions that an execution task composed the next step of the experiment (Hennenlotter et al., 2005; Leslie et al., 2004). During mere observation, brain activations within premotor and parietal regions in these experiments could therefore be biased by the (implicit) attention of the subjects towards their own motor programs. The other viewing tasks that were used (paying attention to the emotion of facial expressions in a delayed match-to-sample task and paying attention to facial motor programs during an imitation task) increased the amplitude and the extent of the activations within the “classical” and “extended” MNS. This finding is at odds with a study by Iacoboni et al. (2005), which did not report differences in “classical” MNS activations due to differential task instructions during the observation of actions, so further studies will be necessary to resolve this discrepancy. The motor response requirement in our discrimination and imitation task but not our observation task may have been a factor in explaining the higher activations during the discrimination and imitation tasks. It should be noted, however, that our results suggest on the one hand that the MNS is recruited even in the absence of an explicit task but on the other hand that it can be modulated by instructions. The MNS may thus be “automatic” only in the sense of being recruited without explicit instructions or efforts, but not in the strong psychophysical sense of being immune to attention modulation.

Interestingly, only a very limited number of studies have investigated the issue of biological motion specificity within the MNS (Schubotz & von Cramon, 2004). We have shown biological specificity in parts of the MNS, as specific sites within inferior frontal cortex showed more involvement during the observation of moving faces than moving patterns. In addition, the pre-SMA, STS and amygdala also showed more activation during the observation of moving faces than moving patterns. Since we only compared pattern motion with a single category of biological motion, it is impossible to conclude from our data whether brain regions located through this analysis show true specificity for facial actions or specificity for more general biological motion. Interestingly, parietal regions showed greater activity during pattern motion observation than during facial movement observation. This finding

is in apparent contrast with monkey single-cell data, which showed the presence of mirror neurons in the inferior parietal lobule that responded both to the execution of a particular action and the observation of a similar action (Fogassi & Luppino, 2005). Moreover, several neuroimaging studies in humans have shown congruent mapping of particular motor actions during both execution and observation in the parietal cortex (see Rizzolatti & Craighero, 2004, for a review). A possible explanation for the higher parietal activation during pattern viewing compared with face viewing could be that since the moving patterns were less familiar to our subjects, pattern processing had to draw more heavily on attentional resources like the parietal cortex. Face processing on the other hand could occur in more specialized regions like the Fusiform Face Area (FFA; Kanwisher et al., 1997).

One of the fundamental pillars of the mirror-matching hypothesis of emotion attribution from faces is that a specific observed expression is being transformed into a motor and/or affective and/or somatosensory representation similar enough to this observed expression to understand the emotion. So far, only one study has examined the MNS using different emotions (Wicker et al., 2003). A major aim of our study was therefore to take a careful look whether fMRI can provide evidence of this selective mapping property in the brain. In order to accomplish this, we used several different facial expressions including a neutral facial condition that also contained facial dynamics. The inclusion of facial dynamics in our neutral condition is crucial in limiting the motion confound contrasting moving emotional expressions with immobile neutral expressions as present in previous studies (e.g., Hennenlotter et al., 2005).

Prime candidates for finding facial expression specificity in the MNS are sub-regions of the premotor cortex that map the different expressions, and limbic brain regions more intimately linked with specific emotions, e.g., amygdala and insula (Calder et al., 2001; Goldman & Sripada, 2005; Keysers & Gazzola, 2006). The “classical” mirror neurons in the premotor cortex could map the motor aspects of witnessed facial expressions (Leslie et al., 2004), while limbic regions could contain mirror neurons resonating the emotion behind the facial expressions (Carr et al., 2003; Wicker et al., 2003; see also Figure 1). In this study, we found emotional facial expressions compared with a neutral dynamic expression to

activate premotor, insula and pre-SMA regions during both observation and execution. On the other hand, SI and SII were more strongly activated to neutral facial expressions compared to emotional facial expressions during both observation and execution. Stronger somatosensory activations during the observation and execution of blowing up the cheeks might be a reflection of the accumulation of tension around the mouth region while the cheeks are being inflated. This type of sensory information is processed through extero- and proprioceptive pathways, which eventually terminate in parietal somatosensory cortex such as SI and SII (Craig, 2002). Our finding of differential processing of neutral and emotional facial expressions in the brain is important, as it shows that the brain discriminates between neutral and emotional facial movements within specific brain regions in a congruent manner. Understanding other people from facial expressions might thus be a combined endeavor of simulation processes within different modalities: somatosensory, motor and limbic systems are all important. Simulation processes within all of these individual systems have been described previously (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Keysers et al., 2004; Wicker et al., 2003). At the neuronal level, premotor mirror neurons might resonate the facial movement and its implied intention (Carr et al., 2003; Iacoboni et al., 2005), insula mirror neurons might process the emotional content (Wicker et al., 2003), and somatosensory neurons might resonate proprioceptive information contained in the observed facial movement (Keysers et al., 2004). This process fits with the theories of facial expression understanding (Adolphs, 2006; Carr et al., 2003; Leslie et al., 2004) as it proposes that several brain systems corroborate during the reading of facial expressions. Premotor cortex, insula and somatosensory regions can resonate while observing facial movements in other people, the amount and pattern of activation within each system depending on what expression is being witnessed.

However, the picture of the understanding of facial expressions by the MNS remains incomplete, as differences between individual emotional facial expressions within the MNS were minor. Disgust specificity in the insula and fear specificity in the amygdala could not be established. Studies have found specificity for individual emotions and sensations at the neuronal level in amygdala (Paton, Belova, Morrison, &

Salzman, 2006) and IFO (Scott & Plata-Salaman, 1999). However, neurons that code for opposite emotional valences were found side by side within the spatial resolution that would correspond with an fMRI voxel. In that case, the fMRI BOLD response will be unable to differentiate between neural activations due to different emotional valences. fMRI might therefore not be a very suitable technique to solve the specificity problem, new paradigms or other techniques are necessary to look more careful into this issue. Another limitation of our study is the limited self-relevance of the stimuli we used for the subjects, although we believe that the range of dynamic stimuli we adopted is still more suitable for studying the MNS than the still pictures and the restricted number of dynamic stimuli implemented in previous studies. In addition, although our execution part of the study might be reasonable in studying the motor aspects of the MNS, the study of emotional aspects is questionable as we asked subjects to generate emotional feelings by a cognitive induction method. A more natural induction of emotions during scanning is a difficult but essential next step in establishing emotional resonance within the brain (Wicker et al., 2003).

Strikingly, the pre-SMA showed up in all our analyses: it is spontaneously active during facial expression observation even in the absence of an explicit task, it responded more to the vision of facial movements than pattern motion and it responded more strongly to the observation and execution of emotional facial expressions than neutral facial expressions. Recent research has reported an anatomical and functional distinction between the pre-SMA and the SMA proper. While the more rostral pre-SMA might be more involved in the preparation and selection of the future execution of movements, the more caudal SMA might be more closely tied to the actual execution of movements (Cunnington, Windischberger, & Moser, 2005). A similar distinction in the function of pre-SMA and SMA-proper can be applied to the domain of language as well (Alario, Chainay, Lehericy, & Cohen, 2006), where pre-SMA is involved in the selection of words and SMA-proper in their production. It is interesting that surgical lesions to the (pre-)SMA have been reported to lead to impairments in the production of emotional facial expressions while other facial movements were less affected (Laplaine, Talairach, Meininger, Bancaud, & Orgogozo, 1977). Some discussion, however,

exists on whether the (pre-) SMA is crucial for the execution of emotional facial expressions as it has been hypothesized that a more ventral region in the anterior cingulate cortex might be responsible for difficulties in expression production (Morecraft, Stilwell-Morecraft, & Rossing, 2004). Recently, it has also been speculated that the pre-SMA is involved in attention to timing aspects of stimuli (Coull, Vidal, Nazarian, & Macar, 2004) and the representation of intention (Lau, Rogers, Haggard, & Passingham, 2004). These functions do not contradict the possibility that the pre-SMA contains mirror properties, as is suggested by the results of our study. In monkeys, the homologue of area pre-SMA (Area 6 $\alpha\beta$ or F6) shows complex neural responses that suggest that it may modulate ventral premotor cortex depending on whether an action is appropriate within a certain context or not (Rizzolatti et al., 1990). However, single-cell studies in this structure during action observation have, to our knowledge, not yet been performed. It may thus be that pre-SMA exerts a modulatory function on the ventral premotor MNS, for instance by inhibiting inappropriate imitation, in analogy to its modulatory function during action execution, or contain mirror neurons itself. By using depth electrodes, Krolak-Salmon et al. (2006) showed that the pre-SMA in humans is selectively activated during both the observation and production of happy facial expressions. We could not replicate this promising finding of selectivity in the pre-SMA for happy facial expressions, differences in spatial resolution between the depth electrode technique and fMRI voxels could account for this discrepancy. As single-cell studies of the pre-SMA in monkeys and humans are lacking, conclusions about the mirror properties of this structure remain tentative.

In conclusion, findings from this study are encouraging, despite the limitations outlined before. In short, the “classical” mirror neuron system (composed of premotor and parietal areas), limbic regions and the somatosensory system become spontaneously active during the monitoring of facial expressions and the production of similar facial expressions. Restricted regions of this extensive network are selective for biological motion. Although we did not find evidence on the selectivity for specific emotions in the “classical” and “extended” MNS, we report a congruent discrimination between blowing up the cheeks (our neutral condition) and emotional facial expressions. Premotor and insula

regions are more involved in the observation and execution of emotional facial expressions, while somatosensory regions are more active during the witnessing and production of blowing up cheeks. Based on our findings, the understanding of facial expressions of other people may be best conceived as involving a combined effort of simulation processes within motor, limbic, and somatosensory systems. This process might reflect the translation of the motor program, emotions and somatosensory consequences of facial expressions, respectively (Keysers & Gazzola, 2006). Through these processes we might translate the bodily and emotional states of others into our own. Understanding the simulated state of the other then boils down to understanding our own states, a process that probably requires additional neural circuits (Keysers & Gazzola, 2007).

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A BRIEF GUIDE TO THE APPENDICES

Appendix 1. Illustration of the tracing of the amygdalae in the 17 subjects.

1. Facial Execution

Appendix 2. Areas of increased signal during the execution of facial expressions.

Appendix 3. Results of facial expression imitation (combining all facial conditions – rest) as shown by a random effects analysis of 17 subjects.

Appendix 4. Comparisons of emotional and neutral execution (combining all emotional facial conditions – neutral facial condition) as shown by a random effects analysis of 17 subjects.

Appendix 5. Areas selectively involved in the production of one facial condition compared to the remaining facial conditions (execution specificity).

2. Task influences

Appendix 6. MNS analyses during the different task conditions.

Appendix 7. Brain regions that significantly differentiate between facial viewing tasks inclusively masked with facial expression production.

3. Biological specificity

Appendix 8. Brain regions that significantly differentiate between dynamic faces and dynamic patterns during the passive Observation (1) and the Discrimination (2) task, inclusively masked with facial expression production.

4. Facial condition specificity

Appendix 9. Emotional and neutral facial expression processing in the MNS.

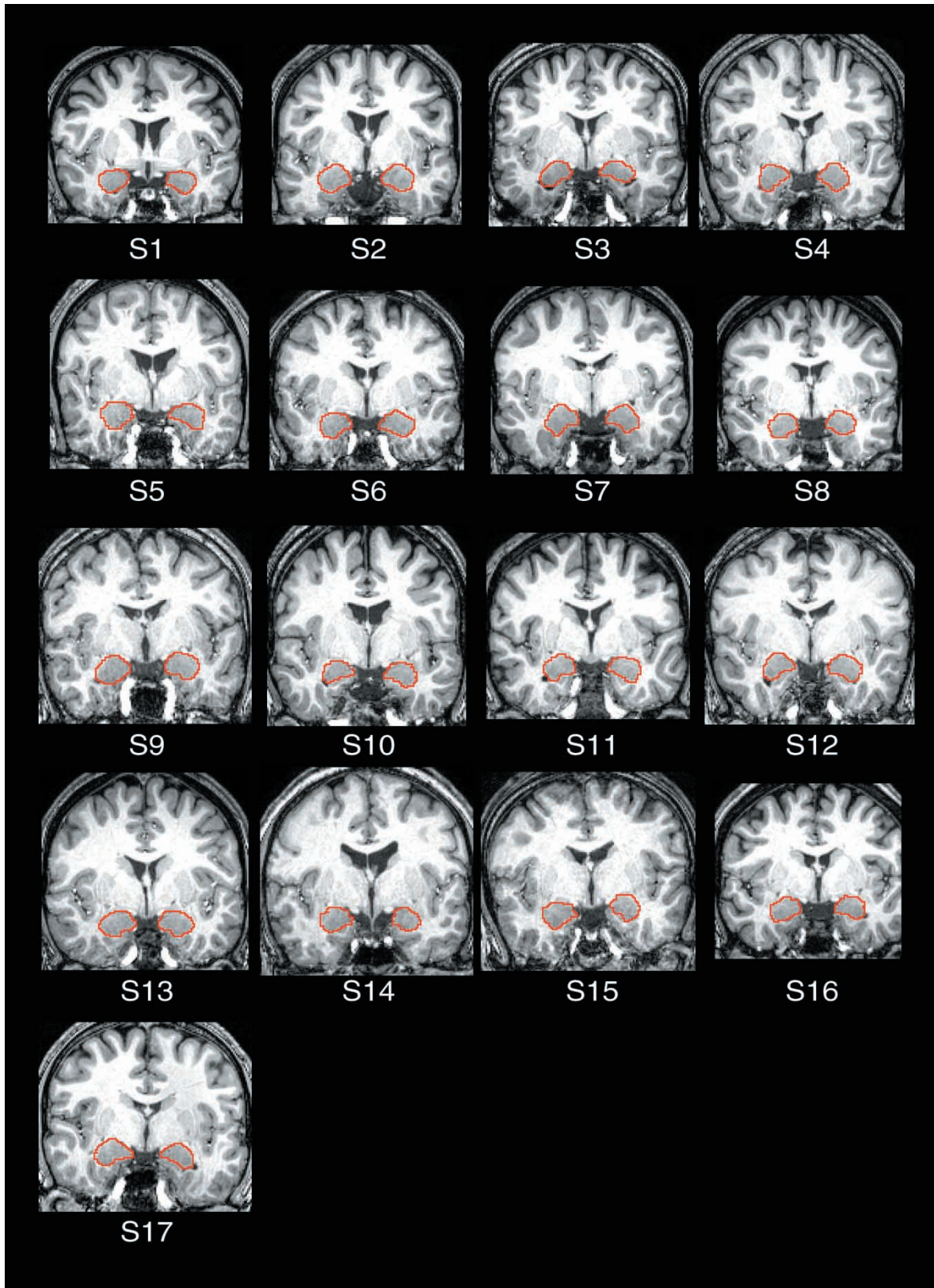
Appendix 10. Contrast values of the different viewing and execution conditions from remaining ROIs which were not shown in Figure 6.

Appendix 11. Signal increases for the contrast Emotional facial condition minus Neutral facial condition during the viewing condition (combining observation and discrimination) for consecutively, the disgusted (A), fearful (B) and happy (C) expressions.

Appendix 12. Specificity for individual facial conditions within the MNS.

APPENDIX 1

(See p. 204 for caption.)



APPENDIX 1 (previous page)

Illustration of the tracing of the amygdalae in the 17 subjects (S1 . . . S17). A coronal slice running approximately through the middle of the amygdalae is shown for each subject. The red contour delineates the outside border of the traced region, being the first voxel outside of the traced amygdalae.

APPENDIX 2 (opposite)

Areas of increased signal during the execution of facial expressions.

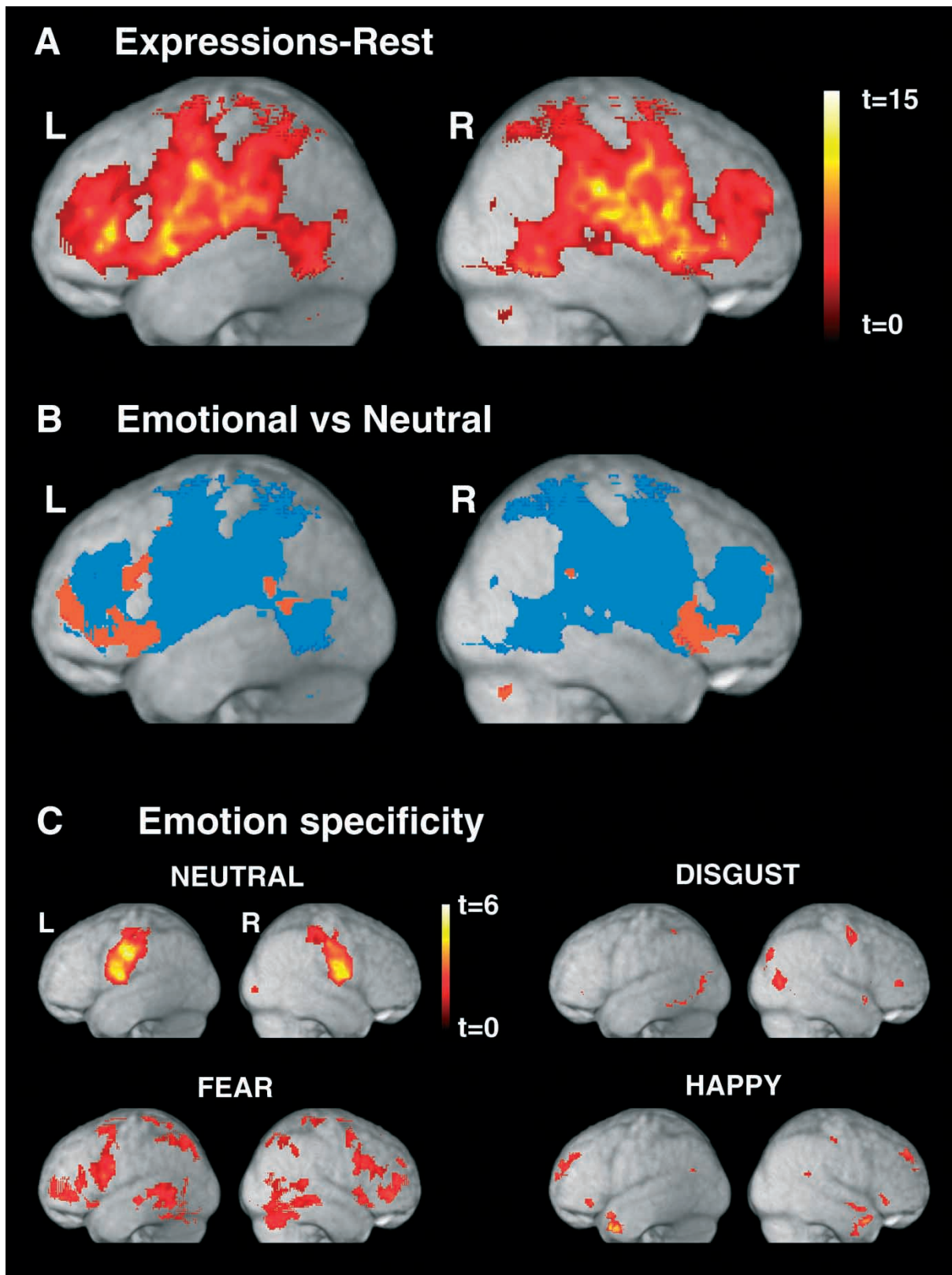
(A) Shows those brain regions that are active during facial expression execution [all four facial conditions combined – rest, $t(16) > 2.92$, $p < .005$, $k = 20$]. Maps are shown with the same threshold as used for the inclusive masking for our MNS analyses.

(B) The same map as displayed in (A), only separated in areas that are more involved in emotional expression execution than neutral expression execution [three emotional facial conditions combined – rest, $t(16) > 2.92$, $p < .005$, $k = 20$] (in orange) and areas which do not differentiate between emotional and neutral expression execution [three emotional facial conditions combined – rest, $t(16) < 2.92$, $p < .005$, $k = 20$] (in blue).

(C) Areas selectively involved in the production of one facial condition compared to the remaining facial conditions (execution specificity). Pair-wise contrasts between the target emotion and the three remaining facial conditions were calculated ($p < .1$). In addition, the parameter estimate of the target emotion needed to be above zero at $p < .05$. Requiring that these four tests be significant results in a false positive rate under a global null hypothesis of $p_{\text{global}} < .1^3 \times .05 = .00005$ (see also the Materials and methods section). See Appendices 3, 4, and 5 for coordinates of local maxima.

APPENDIX 2

(See opposite for caption.)



APPENDIX 3

Results of facial expression imitation (combining all facial conditions – rest, $p < .005$, $k=20$) as shown by a random effects analysis of 17 subjects. For each cluster, from left to right, we describe: the hemisphere containing the cluster; the anatomical and/or cytoarchitectonic description of the cluster, based on the anatomy toolbox provided by Eickhoff et al. (http://www.fz-juelich.de/ime/ime_brain_mapping); the number (k) of $2 \times 2 \times 2$ voxels contained in the cluster (if available); the uncorrected p -value (if available), corresponding t -value and the MNI coordinates of the peak voxel. Activations are presented per cluster and, if possible, are first shown for the regions of interest of this paper (premotor regions in inferior frontal cortex, BA 44/6 and BA 45, STS/MTG, posterior parietal cortex, motor regions and limbic regions like, insula, amygdala)

Hemisphere	Anatomical description	k	p (uncorr.)	t	MNI		
					x	y	z
Right	BA 44			13.31	56	8	18
Right	Area 6			12.03	12	-2	68
	Area 6			11.65	6	-4	64
	Area 6			10.85	12	4	72
Right	Area 6			8.59	28	-10	50
				6.55	32	0	50
Right	Area 6			8.15	22	-18	62
				6.15	22	-18	74
Right	Inferior frontal (p triangularis)			7.44	44	36	26
				7.14	42	36	18
Left	Inferior frontal (p triangularis)			12.58	-48	36	6
	Idem			11.09	-44	40	0
	Idem			8.79	-52	38	0
	BA 45			8.39	-42	46	18
Right	Middle temporal gyrus			8.35	58	-56	-2
	Inferior temporal gyrus			8.28	56	-58	-12
	Middle temporal gyrus			6.41	56	-62	6
Right	Middle temporal			7.49	46	-40	2
Right	Postcentral gyrus			10.67	24	-46	66
	Precuneus			10.36	8	-38	52
	Superior parietal			10.03	16	-60	60
	Superior parietal			9.25	18	50	54
Right	Supramarginal gyrus			14.90	58	-28	26
Left	Inferior parietal			7.73	-36	-48	40
	Middle occipital			7.39	-28	-56	36
	Inferior parietal			7.39	-36	-52	54
	Superior parietal			6.66	-28	-62	52
Left	Cuneus			7.60	-10	-82	34
	Idem			7.45	2	-80	38
	Idem			6.50	-6	-82	26
Left	Middle cingulate			9.70	-14	-32	42
	4p			9.49	-18	-30	60
	4p			8.77	-16	-46	62
	Superior parietal			7.98	-20	-54	62
Right	Insula			12.13	30	18	6
Right	Insula			10.57	40	-4	2
Right	Insula			9.91	40	2	6
Left	Superior temporal gyrus			12.48	-56	4	-2
	Pallidum			11.77	-24	0	-2
	Insula			11.50	-38	-6	-6
	Insula			11.30	-34	8	6
	Area 4 p			11.49	-54	-8	38
	L inferior frontal gyrus (opercularis)			11.40	-58	6	8

APPENDIX 3 (Continued)

<i>Hemisphere</i>	<i>Anatomical description</i>	<i>k</i>	<i>p (uncorr.)</i>	<i>t</i>	<i>MNI</i>		
					<i>x</i>	<i>y</i>	<i>z</i>
	OP1			11.45	-58	-22	14
	OP4			10.61	-56	-12	12
	Thalamus			11.45	-14	-14	2
Right	Middle cingulate cortex			11.53	6	20	30
Left	Middle cingulate cortex			13.82	-6	8	42
Right	Middle frontal			8.63	28	52	22
	Idem			8.00	32	40	28
Left	Middle frontal			6.59	-40	38	30
				6.54	-32	38	28
				6.57	52	-30	52
				6.35	14	-82	36
				6.26	18	-76	32
Right	Putamen			11.45	18	10	-2
Right/Left	Cerebellum Areas 17, 18 Fusiform gyrus	88 591	.000	15.62	28	-48	-34

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APPENDIX 4

Comparisons of emotional and neutral execution (combining all emotional facial conditions – neutral facial condition, $p < .005$, $k = 20$) as shown by a random effects analysis of 17 subjects (for an explanation of the different columns see Appendix 3)

Hemisphere	Anatomical description	<i>k</i>	<i>p</i> (uncorr.)	<i>t</i>	<i>MNI</i>		
					<i>x</i>	<i>y</i>	<i>z</i>
<i>Emot-N</i>							
Right	Inferior frontal gyrus (p triangularis)/BA 45	1138	0	5.37	48	32	-2
	BA 44			4.98	56	20	6
	Insula			4.82	42	18	-6
Left	Inferior frontal gyrus (p orbitalis)	2574	0	5.96	-44	28	-6
	Middle frontal gyrus			5.10	-40	52	8
	Inferior frontal gyrus(p opercularis)			4.57	-40	14	18
	Middle orbital gyrus			3.93	-42	44	-8
	Insula			3.90	-26	22	-14
Right	Superior temporal gyrus	139	0	4.95	48	-24	-2
	Also MTG						
Left	MTG/STS	234	.001	3.98	-50	-62	12
Right	Supramarginal gyrus	31	.001	3.56	64	-40	26
Right	Precentral gyrus	25	.001	3.57	46	6	46
Right	Area 6	139	0	4.07	24	-26	64
	Area/3a/3b/4p/2						
Left	Area 6	72	.001	3.53	-18	-26	64
	Area 3b/4a/4p						
Right	Anterior cingulate cortex	121	0	4.42	2	36	0
Left	Anterior cingulate cortex	99	.001	3.89	-6	40	10
Right/Left	Anterior cingulate cortex	25	.001	3.58	6	12	26
Left	Middle cingulate cortex	1447	0	4.80	-4	30	32
Left	Middle cingulate cortex			5.17	-4	-20	32
Right	Pre-SMA			3.73	6	20	56
Left	Pre-SMA			4.19	2	20	48
Right/Left	Hypothalamus	120	0	4.39	-2	-10	-9
Right	Superior medial gyrus	53	0	3.51	10	60	34
Right	Middle frontal gyrus	47	.001	3.73	30	54	22
Left	Middle frontal gyrus	49	.002	3.46	-28	30	20
Left	Cerebellum	90	0	4.41	-22	-68	-40
Right/Left	Cerebellum	10 642	0	7.28	2	-72	-30
	Area 17			6.2	-12	-52	2
<i>Neutral-E</i>							
Right	OP4	1323	0	7.11	60	-8	12
	1/2/3a/3b						
Left	Area 1	1709	0	7.29	-62	-16	34
	OP4/2/3a/3b						
Right	OP3	163	0	6.02	38	-6	16
Right	Cerebellum	50	0	4.32	20	-62	-22
Left	Cerebellum	39	0	4.13	-16	-64	-24
Right	Pallidum/amygdala	32	0	4.39	28	-8	-6
Right	Middle occipital gyrus/Area 18	28	0	5.08	34	-92	2

APPENDIX 5

Areas selectively involved in the production of one facial condition compared to the remaining facial conditions (execution specificity). Pairwise contrasts between the target emotion and the three remaining facial conditions were calculated ($p < .1$). In addition, the parameter estimate of the target emotion needed to be above zero at $p < .05$. Requiring that these four tests be significant results in a false positive rate under a global null hypothesis of $p_{\text{global}} < .1^3 \times .05 = .00005$, see also material and methods (for an explanation of the different columns see Appendix 3)

Hemisphere	Anatomical description	k	t	MNI		
				x	y	z
<i>Neutral</i>						
Right	Area 3b Also OP4/4a/4p/1/2	1945	4.89	58	-4	20
Left	Area 1 Also OP4/4a/4p/3b/2	2592	5.89	-60	-12	36
Right	Insula Also OP3	169	3.59	38	-8	8
Right	Cerebellum	98	3.65	20	-62	-22
Left	Cerebellum	98	3.47	-16	-64	-24
Right	Inferior/middle occipital gyrus	30	1.97	32	-94	-2
Right	Pallidum	28	2.34	28	-10	-4
Left	Putamen	24	1.92	-26	-8	-12
<i>Disgust</i>						
Right	Inferior frontal gyrus (p triangularis/opercularis)	58	2.15	42	16	8
Right	Area 6	124	2.48	40	-6	56
Left	Inferior frontal gyrus (orbital)	59	2.71	-30	38	-4
Right	Inferior parietal lobule	149	2.35	28	-50	52
Left	Superior parietal lobule	198	2.51	-32	-50	56
Right	Area 3a/4p	74	2.27	32	-20	40
Right	Insula	39	2.08	42	10	-12
Left	Insula	39	2.32	-36	-10	-4
Right	SMA/cingulate gyrus	52	2.11	10	14	46
Right	Putamen	23	2.00	16	16	-4
Left	Putamen	213	2.13	-18	6	-6
Right	Middle frontal	60	2.54	40	42	6
Right	Thalamus	212	2.01	18	-14	10
Right	Thalamus	31	2.26	6	-10	-2
Left	Inferior temporal gyrus/fusiform	62	2.61	-46	-42	-16
Left	Middle occipital gyrus	61	1.94	-38	-62	2
Left/Right	Lingual gyrus Also calcarine/17/18	4387	4.03	-18	-62	-6
Left/Right	Cerebellum	698	3.69	16	-66	-40
<i>Fear</i>						
Right	Inferior frontal gyrus (p triangularis) Also 44/45	625	2.62	44	12	24
Right	Inferior frontal gyrus (p opercularis) Also area 44	146	2.58	52	18	-6
Right	Area 6	126	2.69	14	-22	64
Left	Precentral gyrus Also 44/6/45	1537	3.63	-42	0	26

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APPENDIX 5 (Continued)

<i>Hemisphere</i>	<i>Anatomical description</i>	<i>k</i>	<i>t</i>	<i>MNI</i>		
				<i>x</i>	<i>y</i>	<i>z</i>
Left	Inferior frontal gyrus (p triangularis)	248	3.06	-38	34	8
Left	BA 45	68	2.22	-52	32	16
Left	MTG	276	2.76	-48	-50	0
Left	Inferior parietal Also middle/superior occipital gyrus	558	2.05	-30	-72	44
Left/Right	Precuneus Also 4a/6/3b Inferior parietal cortex	1643	2.77	-8	-52	72
Left	Amygdala Also hippocampus	135	2.13	-18	2	-20
Right	Hippocampus	149	1.94	24	-22	-14
Right	Superior medial gyrus	121	2.05	6	32	48
Right	Middle frontal gyrus	120	2.10	42	8	58
Left/Right	Thalamus	36	1.75	2	-6	6
Right	Cerebellar vermis	1498	2.99	2	-50	2
<i>Happy</i>						
Right	STG	20	1.91	54	-46	18
Right	Middle temporal gyrus Also superior temporal gyrus	111	2.86	58	-2	-14
Right	3b Also 4a	37	1.95	42	-20	52
Right	Inferior frontal (orbital)	59	2.07	40	30	-10
Left	Inferior frontal (orbital)	50	2.95	-40	32	-10
Left/right	Mid orbital gyrus Also superior medial	1518	4.81	-4	50	-6
Right	Anterior cingulate	25	1.58	4	26	20
Right	Medial temporal pole	211	3.88	50	12	-28
Left	Medial temporal pole	134	4.48	-42	14	-34
Right	Caudate	57	2.55	16	18	12
Left	Caudate	40	1.86	-4	12	-2
Left	Putamen	22	1.46	-28	12	-6
Left	Thalamus	24	2.11	-22	-26	0
Left	Precuneus	75	2.51	0	-68	28
Left	Middle occipital gyrus	22	2.05	-38	-66	24

APPENDIX 6

MNS analyses during the different task conditions. Reported brain regions are active during facial expression viewing, all four facial conditions combined – rest, $t(16) > 2.92$, $p < .005$, $k = 20$, inclusively masked with facial expression execution, all four facial conditions combined – rest, $t(16) > 2.92$, $p < .005$. The same analysis was consecutively performed for (1) passive observation; (2) discrimination; and (3) viewing-before-imitation as viewing conditions. Moderate thresholds of both (viewing and production) group t -maps ($p < .005$) were combined, resulting in an overall false positive under a global null hypothesis of $p < .000025$ (for explanation of the different columns see Appendix 3)

Hemisphere	Anatomical description	k	t	MNI		
				x	y	z
<i>(1) Observation</i>						
Right	Middle frontal gyrus	2612	7.18	48	8	52
	Including: BA 44		6.72	50	16	26
	BA 44		6.71	52	14	14
	BA 45		6.70	48	22	-4
	BA 45		6.54	50	22	24
	BA 45		6.43	52	26	-2
Left	Insula	1251				
	BA 45		7.33	-52	38	6
	Including: BA 45		6.05	-54	30	8
	BA 45		5.18	-52	26	26
	BA 44		4.99	-46	12	28
	BA 44		4.93	-42	12	26
Right	Left inferior frontal gyrus (p orbitalis)	671	4.85	-48	20	-10
	Left insula					
	Inferior parietal lobule		6.10	34	-50	50
	Including: right superior occipital gyrus					
Left	Right angular gyrus	537				
	Right superior parietal lobule					
	Inferior parietal lobule		4.82	-34	-56	50
Right	Including: left superior parietal lobule	488				
	Left angular gyrus					
Right	Area 6	37	4.75	10	6	72
	Including: (Pre-) SMA		4.44	4	20	60
Left	Middle frontal gyrus	15 068	3.91	-46	6	52
	Including: area 6					
Left/Right	Precentral gyrus	15 068				
	Fusiform gyrus		12.19	-20	-86	-18
	Also right MTG		11.14	62	-48	16
	Right fusiform		11.05	34	-76	-18
	Left cerebellum		10.58	-36	-60	-22
	Right amygdala		9.70	20	-2	-18
	Left amygdala		9.32	-14	-6	-16
	Thalamus					
	BA 17/18					
	Hippocampus					
Right	Area 1 (SI)	216	5.05	62	-16	42
	Including: Area 2 (SI)					
Left	Area 1 (SI)	23	5.75	-62	-12	28
Left	Area 17	77	4.38	-10	-76	10
Right	OP3 (SII)	50	4.32	36	-6	12
	Including: Right insula		3.86	40	-4	8
Left	OP4 (SII)	28				
	OP3 (SII)		6.32	-42	-6	18

APPENDIX 6 (Continued)

<i>Hemisphere</i>	<i>Anatomical description</i>	<i>k</i>	<i>t</i>	<i>MNI</i>		
				<i>x</i>	<i>y</i>	<i>z</i>
<i>(2) Discrimination</i>						
Right	Inferior frontal gyrus (p opercularis)		7.20	48	16	28
Left	Inferior frontal gyrus (p triangularis)		7.96	-34	34	0
	BA 45		6.52	-54	24	26
	BA 44		6.42	-46	14	26
	BA 44/operculum		6.16	-50	10	4
Right	Area 6	85	4.63	18	-26	72
	Including: Area 4a		3.71	12	-30	76
Left	Area 6		6.80	-26	-24	66
Right	Inferior parietal lobule		6.63	34	-54	54
Left	Inferior parietal lobule		5.86	-32	-58	48
Right	Inferior occipital gyrus	35 637	12.53	22	-28	-4
	Including: Area 6		11.50	58	6	38
	Inferior temporal gyrus		10.86	46	-52	-14
	Area 17					
	STS/MTG R		9.83	60	-38	18
	STS/MTG L		9.56	-54	-50	8
	Thalamus		5.54	-8	-16	0
	Putamen L		6.91	-22	14	-2
	Putamen R		5.97	20	12	-2
	Amygdala L		7.09	-18	-2	-18
	Amygdala R		8.95	26	0	-20
	Insula/operculum L		6.48	-46	16	-2
	Insula L		5.82	-40	6	-2
	Insula R		7.82	46	14	-4
	Area 1/3 L		6.06	-52	-12	50
	Area 2 L		5.79	-46	-32	46
	Area 1/2 R		7.00	52	-26	56
	Area 4p L		5.91	-38	-22	52
Left	Area 4a	62	4.96	-8	-44	64
	Including: Area 3a/3b		4.49	-8	-46	68
Left/Right	SMA L		7.93	-4	10	48
Right	Middle frontal gyrus	26	3.79	32	46	26
Left	Middle frontal gyrus	317	4.70	-26	42	28
Left	Precuneus	36	3.69	-16	-70	36
Right	Cerebellum		6.27	18	-70	-35
Left	Cerebellum		7.75	-12	-84	-37
<i>(3) Viewing – Imitation</i>						
Right	Inferior temporal gyrus	33 139	10.25	46	-52	-14
Right	Including: Area 17/18		6.46	12	-88	4
	STS/MTG R		8.96	58	-38	2
	STS/MTG L		6.67	-58	-44	14
	Thalamus L		8.84	-10	-18	2
	Thalamus R		7.73	18	-22	8
	Putamen L		7.55	-20	8	0
	Putamen R		7.04	20	10	6
	Amygdala L		9.74	-30	-4	-14
	Amygdala R		10.00	22	-2	-20
	Insula/operculum L					

APPENDIX 6 (Continued)

<i>Hemisphere</i>	<i>Anatomical description</i>	<i>k</i>	<i>t</i>	<i>MNI</i>		
				<i>x</i>	<i>y</i>	<i>z</i>
	Insula L		8.09	-28	22	4
	Insula L		8.12	-36	12	4
	Insula R		5.60	34	16	4
	Area 1/3 L					
	Area 2 L		6.18	-42	-32	40
	Area 1/2 R					
	Area 4a L/precentral		5.88	-50	-2	32
	Area 4a R/Area 6		6.56	52	-4	36
Left/Right	SMA L		6.56			
Right	Inferior parietal lobule		5.52	26	-52	44
Left	Inferior parietal lobule		6.63	-32	-50	42
	Superior parietal		8.34	-26	-60	46
Left	BA 44		10.12	-46	16	26
	Inferior frontal gyrus (p triangularis)		10.11	-32	32	-2
Left/Right	Area 6 L	2837	10.67	-21	0	48
	Including: Area 6 R		8.19	4	2	60
Left	Middle cingulate cortex		8.09	-6	14	40
Left	Middle frontal gyrus	254	5.48	-28	40	22
Right	Middle frontal gyrus	71	4.95	30	42	28

APPENDIX 7

Brain regions that significantly differentiate between facial viewing tasks, matched pair *t*-test, $t(16) > 2.92$, $p < .005$, $k = 20$, inclusively masked with facial expression production, all four facial conditions – rest, $t(16) > 2.92$, $p < .005$. The following pairwise comparisons were performed: (1) discrimination contrasted against observation; (2) viewing-before-imitation contrasted against observation; and (3) viewing-before-imitation contrasted against discrimination. Inclusive masking at $p < .005$ of a contrast thresholded at $p < .005$ resulted in an overall false positive rate of $p < .005^2 = p < .000025$ (for an explanation of the different columns see Appendix 3)

Hemisphere	Anatomical description	<i>k</i>	<i>t</i>	<i>MNI</i>		
				<i>x</i>	<i>y</i>	<i>z</i>
<i>(1a) Observation > Discrimination</i>						
No activations						
<i>(1b) Discrimination > Observation</i>						
Left/Right	Area 6/SMA Including: Inferior frontal gyrus (BA 44)/insula	14 472	9.84	58	4	40
Right	Insula	29	3.55	48	14	–4
Right	Amygdala	119	4.55	18	–2	–14
Right	Middle frontal gyrus	112	4.64	32	40	30
Left	Middle frontal gyrus	498	6.61	–36	44	16
Left	Thalamus	484	4.95	–10	–18	2
Right	Thalamus	68	4.07	12	–18	6
Right	Putamen	357	4.96	20	12	–2
Left	Putamen	340	6.68	–22	8	8
Right	Hippocampus	147	8.39	22	–28	–4
Right/Left	Cerebellum MTG/fusiform	10 005	7.69	26	–62	–18
<i>(2a) Observation > Imitation</i>						
Right	Superior frontal gyrus	45	5.57	22	54	32
<i>(2b) Imitation > Observation</i>						
Left/Right	SMA Including: Insula, inferior frontal gyrus (BA 44, BA 45), middle cingulate cortex, thalamus, putamen, Area 17/18	24 284	10.40	–4	8	46
Right	BA 44/45	512	5.11	50	30	14
Right	Precentral gyrus, Area 6, Area 3, 4p, BA 44, OP1, OP4	1495	5.90	50	–4	36
Right	Area 6, Area 4a/4p	82	5.13	18	–24	62
Right	Superior parietal	260	4.42	26	–52	42
Left	Area 3b, 2	31	4.05	–22	–36	64
Left	Amygdala	36	4.55	–30	–2	–32
Left	Middle frontal gyrus	437	5.80	–38	46	18
Right	Middle frontal gyrus	133	6.31	30	40	28
Left	Middle cingulate cortex	42	3.97	–6	–42	52
<i>(3a) Discrimination > Imitation</i>						
Left	Cerebellum	260	7.77	–32	–64	–36
Right	Cerebellum	107	3.99	24	–68	–34
Left	Area 6	56	3.66	–26	–24	70
Left	Area 4	29	3.86	–14	–34	72
	Cerebellar vermis	29	3.99	–2	–46	–10
Right	Cerebellum	24	3.67	8	–70	–38

APPENDIX 7 (Continued)

<i>Hemisphere</i>	<i>Anatomical description</i>	<i>k</i>	<i>t</i>	<i>MNI</i>		
				<i>x</i>	<i>y</i>	<i>z</i>
Left	Area 6	23	3.49	-38	-14	64
Right	Supramarginal gyrus	20	3.75	50	-40	30
<i>(3b) Imitation > Discrimination</i>						
Right	Inferior frontal gyrus/BA 44	89	5.43	52	14	6
Left	Inferior frontal gyrus/BA 44	30	4.13	-60	6	16
Left	Inferior frontal gyrus/BA 44	163	3.34	-42	14	24
Left	Precuneus	47	4.68	-14	-66	32
Left	Precentral gyrus	25	3.98	-36	0	48
Right	Area 4a/p	288	4.22	58	-8	36
Left	Area 1/4p/6	167	4.05	-52	-8	32
Left	Pre-SMA	287	4.49	-8	14	46
	Middle cingulate cortex		3.36	-8	18	34
Left	Putamen	208	5.87	-22	10	4
	Insula		3.56	-30	22	4
Right	Pallidum	81	4.96	18	8	2
Right	Inferior temporal gyrus	23	3.96	48	-52	-14
Left	Cuneus	21	3.42	-8	-78	38
Left	Area 17/18	22	3.69	-8	-64	0
Left	Thalamus	41	3.91	-4	-10	2

APPENDIX 8

Brain regions that significantly differentiate between dynamic faces and dynamic patterns during: (1) passive observation; and (2) the discrimination task, inclusively masked with facial expression production, all four facial conditions – rest, $t(16) > 2.92$, $p < .005$.

Brain regions that prefer the observation of dynamic faces over dynamic patterns, all four facial conditions combined-patterns, matched pair t -test, $t(16) > 2.92$, $p < .005$, $k=20$, for the observation (1a) and discrimination task (2a), respectively. Brain regions that prefer the observation of dynamic patterns over facial expressions, matched pair t -test, $t(16) > 2.92$, $p < .005$, $k=20$, for the observation (1b) and discrimination task (2b), respectively (for explanation of the different columns see Appendix 3)

Hemisphere	Anatomical description	k	t	MNI		
				x	y	z
<i>(1a) Observation: Face > Pattern</i>						
Right	BA 44/45	277	6.67	52	24	-4
Left	BA 44	20	3.18	-52	16	4
Right	Inferior frontal gyrus /BA 45	40	3.74	46	24	20
Left	Inferior frontal gyrus	88	5.11	-42	26	-12
Right	Area 6/pre-SMA	240	5.41	6	6	66
Right	Area 6	32	3.55	52	-2	50
Right	Superior temporal gyrus/MTG	1257	8.67	44	-36	4
Left	Superior temporal gyrus/MTG	47	3.73	-58	-48	14
Right	MTG	30	3.76	52	-58	14
Right	Amygdala/hippocampus	340	6.09	18	-4	-18
Left	Amygdala	238	5.60	-20	-4	-18
	Putamen		3.90	-26	6	-10
Right	Fusiform gyrus	86	4.93	38	-46	-26
Right/Left	Area 17/18	732	6.48	12	-90	8
Right	Cerebellum	51	7.26	18	-76	-38
Left	Cerebellum	215	5.05	-20	-80	-38
<i>(1b) Observation: Pattern > Face</i>						
Left	Precentral Including: BA 44 Area 3a OP4	308	5.48	-54	4	30
Right	Supramarginal gyrus Including: Superior parietal Area 2 Precuneus Inferior parietal	3694	7.43	38	-36	40
Left	Superior parietal Including: Inferior parietal	2958	8.64	-12	-78	50
Right	Superior frontal gyrus/precentral	618	6.29	26	-4	42
Left	Precentral/superior frontal gyrus	457	7.01	-28	-8	56
Left	Insula	52	4.62	-40	-2	6
Right	Inferior temporal gyrus	243	5.60	50	-50	-14
Left	Inferior temporal gyrus	357	7.88	-44	-60	-8
Right	Fusiform	86	6.13	26	-58	-14
Left	Fusiform	125	5.48	-24	-58	-14
Right	Middle cingulate gyrus	105	4.49	14	-34	42
Left	Superior temporal gyrus/OP1	75	4.63	-54	-32	10
Right	Middle occipital gyrus	51	6.92	42	-78	24

APPENDIX 8 (Continued)

<i>Hemisphere</i>	<i>Anatomical description</i>	<i>k</i>	<i>t</i>	<i>MNI</i>		
				<i>x</i>	<i>y</i>	<i>z</i>
Left	Middle occipital gyrus	41	5.34	-38	-80	14
Left	Superior occipital gyrus	35	4.81	-20	-88	32
<i>(2a) Discrimination: Face > Pattern</i>						
Right	BA 45	35	3.71	46	26	-2
Right	Area 6/pre-SMA	54	4.17	4	8	68
Right	Area 6/SMA	26	4.07	6	-20	46
Right	MTG	1201	5.98	62	-40	6
Right	Amygdala/hippocampus	103	5.13	16	-8	-18
Right	Temporal lobe	33	4.90	32	6	-24
Right/Left	Area 17/18	643	7.59	10	-76	-6
Left	Cerebellum	26	3.52	-22	-76	-38
<i>(2b) Discrimination: Pattern > Face</i>						
Right	BA 44	462	8.76	50	6	28
Left	Precentral Including: BA 44	504	5.30	-50	4	38
			5.22	-50	4	38
Right	BA 45/middle frontal	277	4.57	50	38	10
Left	BA 45/middle frontal	232	5.29	-44	50	4
Right	Superior occipital gyrus	4359	11.33	28	-70	44
	Including: Superior parietal Area 2					
	Inferior parietal					
Left	Inferior parietal	3996	9.41	-40	-46	42
	Including: Superior parietal Area 2					
Right	Insula	67	5.17	38	-4	8
Right	Superior frontal gyrus/middle frontal	749	7.66	24	6	60
Left	Superior frontal gyrus	403	5.14	-24	-6	56
Right	Middle cingulate gyrus/superior medial gyrus	159	6.00	6	26	42
Left	Anterior cingulate	67	5.12	-4	14	24
Left	Fusiform	206	7.52	-28	-56	-16
Right	Fusiform	132	6.47	26	-56	-14
Right	Inferior temporal gyrus	281	5.68	52	-50	-14
Left	Inferior temporal gyrus	421	7.01	-44	-60	-8
Left	Precuneus	28	3.88	-14	-44	46
Right	Middle occipital gyrus	27	5.86	42	-80	20
Left	Middle occipital gyrus	44	5.20	-38	-80	12
Left	BA 17/18	29	4.10	-6	-76	16
Left	Thalamus	51	4.37	-10	-24	8

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APPENDIX 9

Emotional and neutral facial expression processing in the MNS. (1a) Direct-matching of emotional facial expressions: regions significantly more active during *emotional* facial expression viewing contrasted against *neutral* facial expression viewing, after combining the observation and discrimination task, average of three emotional facial conditions – neutral facial condition, $t(16) > 2.92$, $p < .005$, $k = 20$, inclusively masked with emotional facial expression production, three emotional facial conditions – neutral facial expressions, $t(16) > 2.92$, $p < .005$. (1b) Direct-matching of neutral facial expressions: regions significantly more active during *neutral* facial expression viewing contrasted against *emotional* facial expression viewing, after combining the observation and discrimination task, average of the neutral facial conditions – three emotional facial conditions, $t(16) > 2.92$, $p < .005$, $k = 20$, inclusively masked with neutral facial expression production, neutral facial conditions – emotional facial expressions, $t(16) > 2.92$, $p < .005$. (2) MNS analyses comparing the viewing of one specific emotional – with neutral facial expressions (combining observation and discrimination) for consecutively the disgusted, fearful and happy expressions, for disgust: disgust viewing – neutral viewing, $t(16) > 2.92$, $p < .005$, $k = 10$, inclusively masked with a congruent contrast for facial expression production, for disgust: disgust execution – neutral execution, $t(16) > 2.92$, $p < .005$. Inclusive masking at $p < .005$ of a contrast thresholded at $p < .005$ resulted in an overall false positive rate of $p < .005^2 = p < .000025$. (3) Specificity for individual facial conditions within the MNS. The target emotion (e.g., fear) against the other facial conditions needed to be significant in each case both during viewing and during production and that both during viewing and production the target emotion by itself exceeded zero, i.e., for fear for instance, we tested F–N, F–H, F–D for viewing and for execution at $p < .1$ and fear by itself for execution and viewing at $p = .05$. Combining these 8 tests leads to a false positive rate under the global null hypothesis of $p < .025 \times 10^{-8}$. Analyses were performed consecutively for neutral, disgust, fear and happy and reported using a spatial threshold of 10 voxels ($k = 10$)

Hemisphere	Anatomical description	k	t	MNI		
				x	y	z
<i>(1a) Direct Matching: Emotional–Neutral (k = 20)</i>						
Left	Inferior frontal gyrus (p triangularis)	121	4.34	–46	24	6
	Including: L inferior frontal (p opercularis)		4.28	–52	10	2
	BA 44		3.97	–46	24	10
	Left insula		3.29	–40	16	–2
Left	SMA	77	3.89	–4	14	60
Right	Insula	73	4.13	38	18	–8
	Including: BA 44		3.48	52	18	–4
	BA 45		3.18	54	26	–2
Right	STS	37	4.59	44	–26	–4
<i>(1b) Direct Matching: Neutral – Emotional (k = 20)</i>						
Right	SI	56	4.56			
	SII	78	3.89			
Left	SI	59	4.78			
<i>(2) MN Regions: Emotion–Neutral (k = 10)</i>						
<i>Disgust</i>						
Left	BA 44/BA 45	18	3.95	–44	24	14
Right	Frontal operculum	51	3.90	52	16	–4
	Insula		3.89	40	20	–6
Left	Operculum/insula	210	8.10	–44	20	0
	Operculum		3.55	–52	12	0
Left	Area 6	106	4.4	0	10	64
	Pre-SMA		4.26	–10	12	52
Left/Right	Middle cingulate gyrus	60	5.70	–6	28	32
Right	Middle occipital gyrus	17	3.53	38	–70	2
Left	Superior occipital gyrus	11	3.55	–22	–86	28
Right	Cerebellum	11	3.21	24	–72	–36
<i>Fear</i>						
Right	BA 44	12	3.40	56	16	2
Left	BA 44	27	3.68	–52	12	4
Left/Right	Pre-SMA	54	3.62	–2	18	46
Left	Cerebellum	34	5.38	–40	–66	–28
<i>Happy</i>						
Left	BA 44	13	3.69	–54	22	12
Right	Superior temporal gyrus	37	4.36	52	–24	–4

APPENDIX 9 (Continued)

Hemisphere	Anatomical description	k	t	MNI		
				x	y	z
Right	Superior medial gyrus	12	4.45	10	56	30
Left	Anterior cingulate gyrus	12	3.77	-2	40	10
(3) Emotion Specificity (k = 10)						
<i>Neutral</i>						
Right	Area 6	15	1.84	60	2	28
Right	Area 2 (SI)	150	1.98	48	-34	56
Right	OP1 (SII)	177	2.73	62	-18	26
Left	Area 2 (SI)	256	2.81	-56	-26	44
	Including: Supramarginal gyrus		2.52	-60	-28	42
	OP1 (SII)		1.49	-56	-22	22
<i>Disgust</i>						
Left	Putamen/globus pallidus	18	2.00	-18	4	-6
Left	Lingual gyrus	31	1.96	-18	-74	-12
Right	Fusiform	28	2.02	26	-62	-10
Right	Middle occipital gyrus	210	2.41	40	-72	8
Left	Middle occipital gyrus	38	2.05	-34	-78	4
Right	Superior occipital gyrus	17	1.80	24	-84	32
Left	Superior occipital gyrus	20	1.91	-16	-88	28
Left	BA 17	30	1.92	-4	-68	-4
Right	Cerebellum	15	1.58	26	-58	-44
<i>Fear</i>						
Right	BA 44/BA 45	17	1.73	52	14	32
Left	BA 44	13	1.63	-48	12	10
Left	BA 44	13	1.59	-58	14	6
Right	Area 6	10	1.59	10	0	72
Left	Middle temporal gyrus	64	2.01	-52	-48	4
Right	Middle frontal gyrus	14	1.66	38	6	46
<i>Happy</i>						
Right	Superior medial gyrus	35	2.37	8	56	30
Right	Superior temporal gyrus	18	1.83	54	-46	18

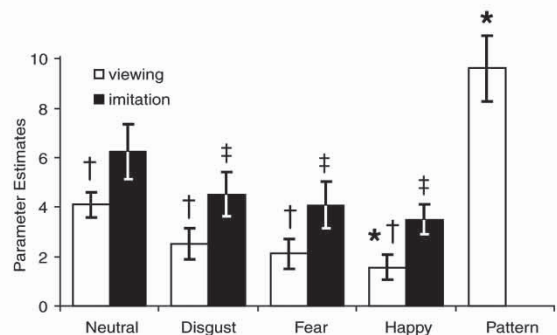
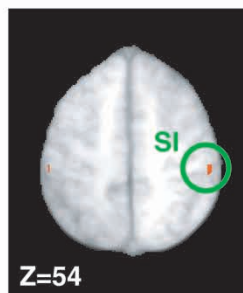
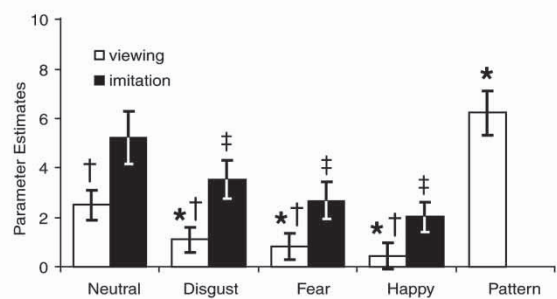
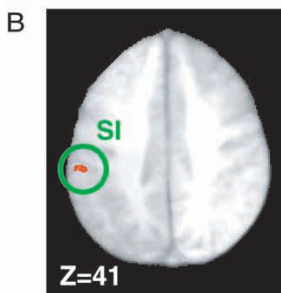
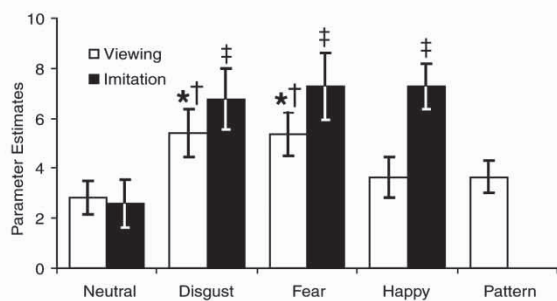
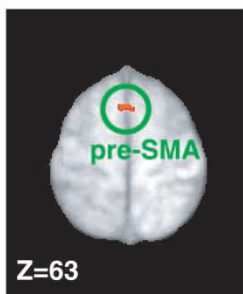
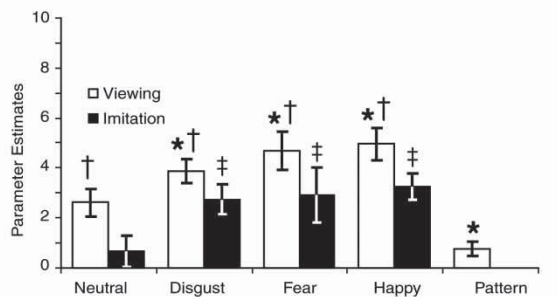
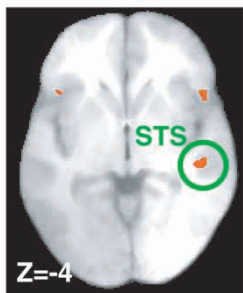
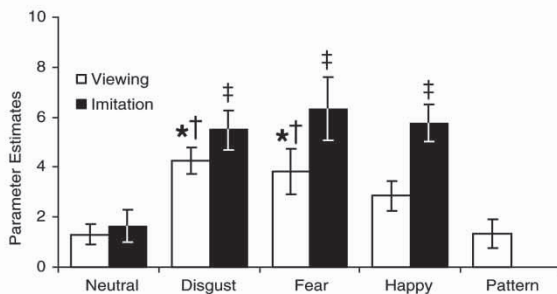
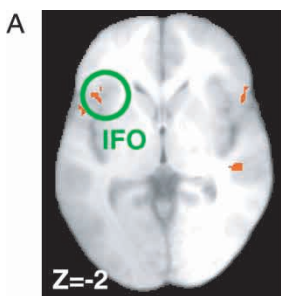
APPENDIX 10 (overleaf)

Contrast values of the different viewing and execution conditions from remaining ROIs which were not shown in Figure 6. Contrast values from the different ROIs were extracted from individual subjects using the Marsbar toolbox (see Materials and methods section).

(A) Left column: Remaining ROIs from the congruent mapping analysis of the Emotional facial expression minus Neutral facial expression contrast, as depicted in Figure 5 and listed in Appendix 9. From top to bottom: left IFO, right STS and bilateral pre-SMA. Right column: Contrast values for the different stimuli during both viewing (combining observation and discrimination) (white bars) and execution (black bars) from our three ROIs. Error bars represent the SEM. The significant main effect of condition (see Results) was further explored using Newman-Keuls post-hoc comparisons: emotional facial conditions that significantly differed from the neutral condition during viewing ($p < .05$) are marked with (*), facial conditions that significantly differed from the pattern condition during viewing ($p < .05$) are marked with (†), emotional facial conditions that significantly differed from the neutral condition during execution ($p < .05$) are marked with (‡). Comparisons of the disgust condition with the remaining facial condition within the IFO (*a priori* hypothesis) is discussed further in the main text.

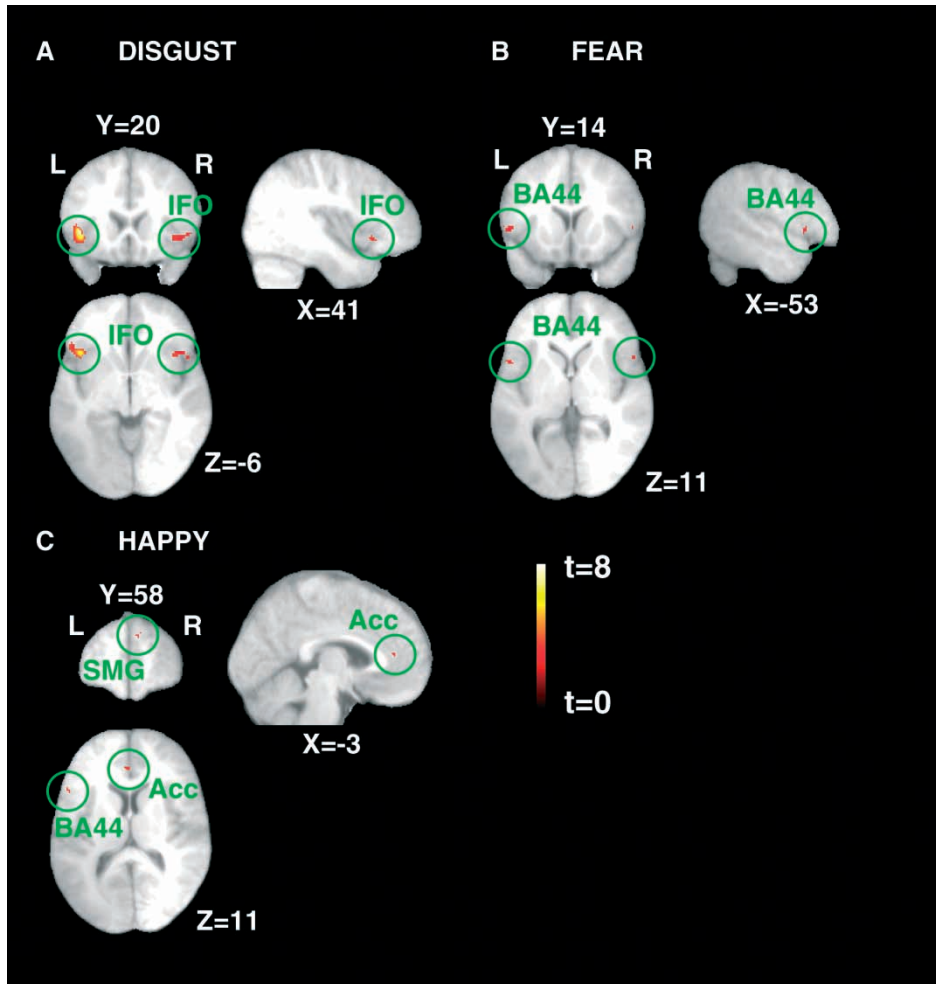
(B) Left column: Remaining ROIs from the congruent mapping analysis of the Neutral facial expression minus Emotional facial expression contrast, as listed in Appendix 9. From top to bottom: left SI and right SI. Right column: contrast values taken from these two ROIs during the different conditions. The same explanation for the graph and the symbols apply as described under (A). IFO, insula/ frontal operculum; STS, superior temporal sulcus; pre-SMA, pre-supplementary motor area; SI, primary somatosensory cortex.

APPENDIX 10



APPENDIX 11

Signal increases for the contrast Emotional facial condition minus Neutral facial condition during the viewing condition (combining observation and discrimination) for consecutively the disgusted (A), fearful (B) and happy (C) expressions (for disgust: disgust viewing – neutral viewing, $t(16) > 2.92$, $p < .005$, $k = 10$). All regions displayed are inclusively masked with a congruent contrast for facial expression production (for disgust: disgust execution – neutral execution, $t(16) > 2.92$, $p < .005$). Inclusive masking at $p < .005$ of a contrast thresholded at $p < .005$ resulted in an overall false positive rate of $p < .005^2 = p < .000025$. Results are overlaid on an averaged T1-weighted 3D render of the 17 subjects. See Appendix 9 for coordinates of local maxima. IFO, insula/ frontal operculum; BA44, Brodmann Area 44; SMG, superior medial gyrus; Acc, Anterior Cingulate Gyrus.



APPENDIX 12

Specificity for individual facial conditions within the MNS. The target emotion (e.g., fear) against the other facial conditions needed to be significant in each case both during viewing and during production and that both during viewing and production the target emotion by itself exceeded zero, i.e., for fear for instance, we tested F–N, F–H, F–D for viewing and for execution at $p < .1$ and fear for execution at .05. Combining these 8 tests leads to a false positive rate under the global null of $p < .025 \times 10^{-8}$. Analyses were performed consecutively for neutral (A), disgust (B), fear (C) and happy (D) and displayed using a spatial threshold of 10 voxels ($k = 10$). Results are overlaid on an averaged T1-weighted 3D render of the 17 subjects. See Appendix 9 for coordinates of local maxima. SI, primary somatosensory cortex; SII, secondary somatosensory cortex; Pt, putamen; BA44, Brodmann Area 44; STS, superior temporal sulcus; SMG, superior medial gyrus.

