Emotion unfolded by motion: a role for parietal lobe in decoding dynamic facial expressions

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Facial expressions convey important emotional and social information and are frequently applied in investigations of human affective processing. Dynamic faces may provide higher ecological validity to examine perceptual and cognitive processing of facial expressions. Higher order processing of emotional faces was addressed by varying the task and virtual face models systematically. Blood oxygenation level-dependent activation was assessed using functional magnetic resonance imaging in 20 healthy volunteers while viewing and evaluating either emotion or gender intensity of dynamic face stimuli. A general linear model analysis revealed that high valence activated a network of motion-responsive areas, indicating that visual motion areas support perceptual coding for the motion-based intensity of facial expressions. The comparison of emotion with gender discrimination task revealed increased activation of inferior parietal lobule, which highlights the involvement of parietal areas in processing of high level features of faces. Dynamic emotional stimuli may help to emphasize functions of the hypothesized ‘extended’ over the ‘core’ system for face processing.

Keywords: dynamic facial expressions; emotion perception; emotion–cognition interaction; inferior parietal lobule

INTRODUCTION

Adequate perception and interpretation of emotional information is a basis for adjustable and appropriate behavior in the everyday social life (Allison et al., 2000; Adolphs, 2002). Understanding other peoples’ intentions requires recognizing their identities and emotions and much of this information is available from faces (Vuilleumier and Pourtois, 2007). Many psychiatric and neurologic disorders are associated with abnormalities in social cognition that have been empirically defined by deficits in the perception of facial expressions (Gur et al., 2002; Schneider et al., 2006; Dyck et al., 2009; Neuner et al., 2010).

Facial expressions like other emotion-eliciting objects have been shown to be processed in a rapid and automatic fashion as indexed by neural and behavioral responses under pre-attentive and even unconscious conditions. This implicit processing enhances the neural response in regions within the visual cortex—including the face-responsive regions—and limbic areas (Breiter et al., 1996; Dolan et al., 1996; Vuilleumier and Pourtois, 2007). However, the explicit appraisal of emotional values—influencing the individual’s perception of environment and the related behaviour—engages a distinctive pattern of neural activity in associative cortical region (Crichtley et al., 2000; Winston et al., 2003). This study sought to elaborate the underlying neural systems in explicit encoding of dynamic facial expressions. We adopted an experimental design, in which the tasks varied between implicit and explicit processing of emotional information whereas the set of stimuli stayed the same. We hypothesized that additional processes such as attention, evaluation, anticipation and top-down control engage a dissociated cortical circuitry during an explicit when compared with an implicit task for emotion processing.

Traditionally, researchers have used static stimuli, such as photographs of human faces to explore the representation and processing of face-related information (Gur et al., 1994; Crichtley et al., 2000; Winston et al., 2003). However, human faces in general and facial expressions in particular are dynamic in nature, which enables an adaptation to situational requirements. It is widely known that temporal properties provide important visual cues in 3D perception and recognition of objects by the human visual system (Marr and Vaina, 1982; Stone, 1998; Vuong and Tarr, 2004). More specifically, it has been shown that temporal cues contribute to the recognition of faces (Pike et al., 1997; Lander et al., 1999; O’Toole et al., 2002; Knappmeyer et al., 2003; LaBar et al., 2003; Sato et al., 2004; Pike et al., 2006) and facial expressions (Bassili, 1978; Christie and Bruce, 1998; O’Toole et al., 2002; LaBar et al., 2003; Sato et al., 2004). Based on this ecological evidence, we assume that dynamic stimuli can enhance the characterization of the brain circuitry that mediates the visual processing of facial expressions. Recent imaging studies have demonstrated that the processing of dynamic facial expressions recruits an extended emotion processing system compared with static facial expressions (Kilts et al., 2003; Trautmann et al., 2009; Rahko et al., 2010). However, the results from direct comparisons of dynamic and static stimuli need to be interpreted with caution, because the inherent properties of dynamic stimuli (i.e. motion and sequential variation) can bias visual attention. This study measured stimulus-locked responses to videos of faces characterizing four levels of emotion and gender intensities. To constrain the number of variable conditions, frame sequences were chosen to depict only two types of emotions with positive (happy) or negative (angry) facial expressions.

It is widely accepted that real face displays potentially facilitate emotion recognition in a more natural way. However, along with the requirements of modern experimental designs for well-controlled stimuli and the improvement of simulation technology computer-generated virtual faces become increasingly popular. Better control over low-level parameters and higher flexibility in manipulation of emotional expressions encouraged us to use the computer-generated face stimuli for this study. Efficiency and validity of virtual emotional expressions for laboratory investigations have been already shown in healthy
populations and patients (Dyck et al., 2008; Dyck et al., 2010). There is also a body of evidence that face recognition system is finely attuned to extract social and emotional information from schematic features (Ohman et al., 2001; Britton et al., 2008; Butler et al., 2008; Evans et al., 2008; Maratos et al., 2008).

MATERIALS AND METHODS

Subjects
Twenty right-handed volunteers (11 female) participated in this study. The participants did not have any history of neurological or psychiatric conditions and ranged in age from 20 to 42 years (mean 28). They all gave informed consent, according to the approval of the local Ethics Committee.

Stimuli
Video presentations of computer-generated faces expressing either happy or angry emotions were generated by Poser Pro 8 (Smith Micro Software, Inc.). The frame sequence started with a neutral face frame, unfolding four levels of emotion intensity during 1 s. Two original faces have been morphed along the emotion and gender dimension at four levels, creating 32 physically different stimuli. We created the morphs for four levels, because in a pilot study, the observers showed difficulties in differentiating more fine-grained steps. Exemplary stimuli are shown in Figure 1.

Task
Prior to scanning, the participants were shown examples of stimuli and were introduced to the procedure. They have been instructed to rank each presentation on an arbitrary scale from 1 to 4 regarding either emotional expression or gender at each time. During scanning, the participants observed the video presentations of centrally located faces. Each presentation took 1000 ms and was then replaced by a blank screen, during which the participants were supposed to deliver their judgment on a scale from 1 to 4 by pressing the response button by index and middle fingers of each hand as fast as possible. The order of buttons was counterbalanced across the subjects. The task alternated between either rating of emotional expression or of gender in subsequent blocks, each preceded by a written instruction indicating which property had to be judged during the upcoming block.

At the end of functional magnetic resonance imaging (fMRI) session, subjects were asked to fill out a debriefing questionnaire and rate the naturalness of happy and angry facial stimuli on a 4-point scale: 1 = very natural, 2 = rather natural, 3 = rather artificial and 4 = very artificial.

Design
The stimuli allowed for evaluation of three factors: task (with two levels: emotion rating and gender rating), emotion type (with two levels: angry and happy) and emotion intensity (with four levels). The $2 \times 2 \times 4$ factorial structure implied 16 experimental conditions which were randomized and presented in an event-related design.

The experiment was divided into four 10-min runs. Happy and angry faces were shown in separate runs since in a pilot study the participant showed difficulties in establishing a constant ranking system when conflicting emotions were intermixed.

Within each run, 160 experimental trials with different levels of emotion and gender were randomly ordered. The basic trial duration was 2700 ms and a stimulus onset asynchrony was secured by random appearance of 50 null events. The total number of 210 trials was equally divided in 14 blocks. Each block started with a written instruction (2000 ms) which cued the task for the subsequent block.

The order of happy and angry runs in the experiment as well as the order of emotion and gender rating blocks within each run was counterbalanced across the participants.

fMRI scanning
Participants were scanned using a 3 T Siemens TRIO system (Erlangen, Germany) to acquire gradient-echo, T2*-weighted echoplanar images (EPI) with blood oxygenation level-dependent (BOLD) contrast [echo time (TE) = 28 ms, matrix size = $64 \times 64$]. Each volume with 42 axial scans and 3-mm in-plane resolution covered the entire brain. For each of the four runs, 254 volumes were acquired (TR = 2500 ms). To allow for T1 equilibration effect, the first four volumes of each run were subsequently discarded. After functional imaging, a T1-weighted structural image was acquired. These structural images were co-registered

Fig. 1 Angry and happy face stimuli at four morph levels were arranged across expression intensity and gender dimensions. Depicted are the final frames for the 1000 ms video displays.
with the mean EPI from the functional acquisition and normalized into a standard space using the normalization parameter applied to the EPIs.

fMRI data analysis

Preprocessing of imaging data and statistical analysis was undertaken using Brain Voyager QX 2.1 (Brain Innovation, Maastricht, The Netherlands). Preprocessing included slice time correction using sinc interpolation, 3D motion detection and correction with rigid body transformations using sinc interpolation to spatially align all functional volumes to the first volume of the last scanning run and high-pass filtering to remove low-frequency drifts (cutoff of three cycles per time course). No spatial smoothing was applied to allow a consistency across uni- and multivariate analysis. The functional volumes were then normalized to an EPI template based on the Talairach reference brain in a standard space (Talairach and Tournoux, 1998) to allow for group analysis.

Statistical analyses were performed using a general linear model (GLM) at the single subject level. Parameter estimates were calculated for each voxel based on design matrices which included predictors for 16 experimental conditions and instruction relative to baseline (null events). In multiple subject analysis, each subject’s predictors entered the GLM calculation separately [random effects (REX) model] and these predictor estimates were used to contrast the main effect of task and intensity. Statistical group maps were generated to represent significant results at the $P < 0.05$ level, corrected for multiple comparisons using cluster-size thresholding (minimal cluster size of 100 contiguous voxels, based on an initial voxel level threshold set at $t \geq 3$).

We performed an additional GLM calculation to evaluate the effect of task difficulty for different experimental conditions, based on the assumption that the differences in reaction times across different conditions correspond to the difficulty of processing. For a ‘reaction-time-modulated’ GLM calculation each of the 16 experimental conditions as regressor was parametrically weighted with the corresponding reaction time (in millisecond) for each experimental condition. This modulation was conducted at the first level of analysis for each subject to ‘regress out’ the confounding influence of task difficulty.

Our design was not optimal for contrasting the main effects of emotion types directly, since happy and angry displays were temporally separated and presented in different runs. However, interactions with the other factors were calculated.

More detailed analyses were performed for the pre-defined regions-of-interests (ROIs) including fusiform face area (FFA) in extrastriate cortex, superior temporal sulcus (STS), amygdale and insula. We used this approach to reduce the probability of false-negative findings. The localization of FFA was based on functional analysis by selecting this approach to reduce the probability of false-negative findings. The cortex, superior temporal sulcus (STS), amygdale and insula. We used of-interests (ROIs) including fusiform face area (FFA) in extrastriate cortex, superior temporal sulcus (STS), amygdale and insula. We used of-interests (ROIs) including fusiform face area (FFA) in extrastriate cortex, superior temporal sulcus (STS), amygdale and insula.

The RFX group maps of the two contrasts of interest were calculated: (i) expression intensity tested by assigning four intensity levels in emotion rating for happy faces 0.59 0.046 emotion rating for angry faces 0.59 0.042 Gender rating for happy faces 0.51 0.035 Gender rating for angry faces 0.51 0.035 Emotional rating for happy faces 0.59 0.046 Emotional rating for angry faces 0.59 0.046

RESULTS

Behavioral

Reaction time

Participants’ reaction times were analyzed by means of repeated-measures analysis of variance (ANOVA) using SPSS (SPSS, Inc., Chicago). This analysis revealed a main effect of task ($F(19), P < 0.001$), indicating a shorter reaction time for gender rating (Table 1).

A significant main effect of emotion intensity ($F(19), P < 0.001$) was due to longer reaction times for judgment of mid-intensity emotions. No main effect of emotion type was revealed but a significant task by emotion interaction effect emerged. The interaction was driven by a facilitation effect in the gender rating of happy faces.

Rating

The rating results across the two different tasks confirmed that the participants succeeded in performing the rating task and tended to assign higher ranks for higher intensities of emotion and masculinity for both emotion types (Figure 2). Performance data at the individual level ensured a consistency across the participants.

Debriefing

Out of 20 observers, 1 person evaluated the computer-generated happy and angry emotions as ‘very artificial’, 5 as ‘rather artificial’ and 14 as ‘rather natural’. Nobody chose the fourth option ‘very natural’.

Imaging

The RFX group maps of the two contrasts of interest were calculated: (i) expression rating vs gender rating based on a GLM contrast collapsed across emotion types and different gender and expression intensities revealed a bilateral activation in inferior parietal lobule (IPL) and (ii) expression intensity tested by assigning four intensity levels in ANOVA model collapsed across emotion types and different tasks showed an activation of hMT+V5, V3a, postcentral gyrus, precentral gyrus, cuneus, precuneus and cingulate (Figure 3 and Table 2). Both contrasts were thresholded at cluster-level (corrected $P < 0.05$, $r(19) > 3$, initial voxel-level $P$-value $< 0.0001$, min cluster size $= 40$ voxels). A RFX group map corresponding to contrast A (expression rating vs gender rating) was calculated based on
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DISCUSSION

This study aimed at understanding how the brain supports the high perceptual capability of extracting face-related information from relevant physical attributes in the context of different task demands. Our paradigm involved higher level visual processing of dynamic faces in the context of gender and expression evaluation. Non-rigid motion is an inevitable property of facial expressions and provides changeable spatio-temporal cues for the visual system. Using a controlled and parameterized paradigm and whole-brain analyses, we could show that in the classic motion-responsive areas such as bilateral hMT+/V5 and right V3a, the BOLD response increased for higher intensities of emotional expressions characterized with a greater motion profile. We also demonstrated that processing of dynamic facial expressions is task dependent and in our paradigm is characterized by an enhanced activation in bilateral IPL. While the role of subcortical regions such as amygdala has been repeatedly shown in emotional processing, these results highlight the involvement of cortical areas in perceptual and cognitive processing of emotions under temporal characteristics of dynamic facial expressions.

Fig. 2 Mean results of ratings. X-axis: four intensity levels. Y: mean rating by participants on a scale from 1–4; n = 20.

Main effect of intensity

Previous findings directly compared the dynamic and static face stimuli and reported an increased activation in distributed brain areas including fusiform and inferior occipital cortex as well as subcortical areas (Kilts et al., 2003; Trautmann et al., 2009; Rahko et al., 2010). We chose an approach, in which we parametrically increased the intensity of dynamic expressions and defined the brain areas with a correlated enhanced BOLD response. For dynamic stimuli, strength of expression signal is inevitably dependent on the motion content. For our stimuli, the emergence of emotional expression through motion activated classic motion-responsive network including hMT+/V5, V3a, cuneus and precuneus along with higher level motion-responsive areas such as pre- and postcentral gyrus, known for sensory-motor integration of
motion-related information (Table 2). In the whole-brain analysis responses of motion sensitive areas to the expression intensity were not affected by the task and thus may be automatic.

Our facial emotion stimulus set activated a bilateral occipito-temporal network, known to be involved in object (and more specific face) and motion recognition as well as a frontolimbic network, which is derived in emotional processing. Furthermore, the majority of observers have interpreted the emotions represented by this stimulus set as rather natural and have successfully differentiated and rated the emotion intensities at the behavioral level. Our fMRI data, however, failed to show the sensitivity of STS, a region involved in processing of body and face motion (Schultz and Pilz, 2009; Peelen et al., 2010) to the intensity of facial expressions (even in the statistic confined to the anatomically defined cluster). One interpretation might be that although STS is specialized in the ‘detection’ of biological movements—including their social aspects—the evaluation of different intensities for dynamic facial expressions is mostly dependent on the non-specialized motion areas. However, it is not entirely clear if the properties of the computer-generated stimuli would drive STS like real biological motion stimuli do. A more detailed ROI analysis of the fMRI data obtained from individuals, who rated the virtual face stimuli as rather natural revealed an emotion intensity effect in right STS. This finding—even though only detectable by a FFX GLM analysis—indicates that an inhomogeneity in appraisal of naturalness of our face stimuli across the subjects may have led to the lack of STS responses in our experiment.

Fig. 3 (Top) RFX group maps of the two contrasts of interest. (Upper row) main effect of emotion intensity shows an enhancement of BOLD responses in a network of motion-responsive areas, including bilateral hMT+/V5, right V3a and postcentral gyrus. No cluster in the whole-brain analysis showed greater response to less dynamic faces, i.e. low intensity > high intensity (P > 0.1). (Lower row) Main effect of emotion rating vs gender rating shows a bilateral activation of IPL. (Bottom) Beta-values extracted from the second level RFX GLM analysis in sample regions confirm a main effect of emotion rating vs gender rating in the bilateral IPL and an interaction effect of valence x intensity in the right postcentral gyrus. GA, gender task/angry faces; GH, gender task/happy faces; EA, emotion task/angry faces; EH, emotion task/happy faces; A1-4, angry faces/intensity 1-4; H1-4, happy faces/intensity 1-4.
The role of face-responsive regions in coding the facial expressions as an intrinsic property of faces has been controversially discussed. Some studies suggested an enhancement in the activity of fusiform extrastriate cortical response to increasing intensities of facial emotions (Surguladze et al., 2003) whereas other studies found no differences in magnitude of this activation for high vs low intensities of facial expressions (Winston et al., 2003). Amygdala connections to visual cortices have been suggested as a possible mechanism for modulation of face-responsive areas by emotion intensity (Vuilleumier and Pourtois, 2007). The ROI-based GLM analysis in this study showed a modulation of BOLD signal in functionally defined FFA by intensity of facial expression. This expected effect could only be shown for right FFA and only with a FEX GLM. Presentation duration is a specific aspect of dynamic stimuli, which most probably serves a main source of heterogeneity across studies.

**Main effect of task**

A critical finding was a task-dependent activation pattern in the whole-brain analysis of fMRI data. During expression evaluation, a bilateral enhanced activation in IPL was observed, which is known to be a common representational domain for perceived events and planned actions (Chong et al., 2008). Activation of these regions in our data supports models postulating that recognition of another individual’s emotion involves simulation of the emotional display (Adolphs et al., 2000). In a social context, recognition of emotional display of a conspecific tightly corresponds to intention detection, anticipation of action and preparing or intending to act. In many psychiatric conditions, deficits in recognition of facial expressions go along with behavioral disturbances such as disorders of empathy and social learning (Dyck et al., 2009; Seifert et al., 2009; Neuner et al., 2010). This perspective implies that decoding of facial expressions requires an extensive interaction of emotion processing system with action representation system and provides an explanation for the enhanced activation of areas in parietal lobe—not primarily involved in emotion processing—during the evaluation of facial expressions.

A distinction between expression-based and gender-based face processing have been hypothesized in previous studies (Critchley et al., 2000; Winston et al., 2003). Therefore, we also considered the task effect for our stimuli, which included the representation of the movement trajectories as critical feature of facial expressions (Table 2). Judgment of expressions evoked significantly stronger BOLD activity in IPL structures, whereas judgment of gender evoked significantly greater activity in early visual areas V1 and V2. Giese and Poggio (2003) have proposed that visual information with shorter time scale is coded by earlier visual areas. Higher order areas that are sensitive to predictability of the trajectories then integrate these low level representations over longer time scales. The distinctive activation patterns in expression-based and gender-based processing of facial stimuli in our data fit into this explanation model. The former processing requires a longer temporal scale which is based on the dynamic representation of trajectories and engages the higher order areas. The activation of early visual cortices in occipital lobe for gender evaluation task might reflect computations over a shorter time scale which is also reflected in the shorter averaged reaction time for rating evaluation of gender.

Facial expressions involve a specialized processing which is independent from other aspects of face recognition (Bruce and Young, 1986). The recognition of emotional expressions in faces has been shown to be preserved in prosopagnosia (face blindness due to lesions in associative visual cortices) (Sergent and Vилlemure, 1989; Duchaine et al., 2003; Humphreys et al., 2007) and in cortical blindness (Morris et al., 2001; Duchaine et al., 2003). We suggest that IPL might constitute a part of the specialized neural system that mediates processing of facial expressions without being involved in face recognition. Our study did not reveal significant differences in the activation of occipito-temporal face-responsive areas as a function of the task. This implies a role in early sensory processing for these areas which is not modulated by appraisal processes.

**Valence-dependent intensity effect**

An interesting interaction effect between emotion type and intensity corresponding to level of aversiveness was revealed in the whole-brain multivariate searchlight mapping. Aversiveness level was considered increasing with the intensity of angry stimuli and decreasing with the intensity of happy stimuli.

While basic properties of dynamic facial expressions, such as emotion intensities activate functionally dedicated regions and can be revealed by activation-based mapping, more socially relevant information of such stimuli seems to be distributed in pattern and therefore best caught with information-based multivariate approaches. Our finding of activation patterns in postcentral gyrus (location of somatosensory cortex), paracentral lobule (location of supplementary motor area), anterior cingulate cortex and precentral suggests that extended cortical networks might be involved in processing of highly integrated social information of dynamic face stimuli with manifold functional and anatomical aspects. These cortical regions are known to be parts of mirror neuron system (Rizzolatti and Craighero, 2004) which explains their involvement in extraction of interactive and social information from faces.

**Organization of human neural system for decoding meaning from faces**

The results of this study suggest that processing of emotional facial expressions extends beyond the cortical areas that respond preferentially to faces. Haxby and colleagues in their influential model stating...
Our results support a necessity for the use of dynamic stimuli in investigations related to facial expressions. The exact role and dynamic of different brain areas and cognitive processes in recognition of facial expressions is far from settled, but our results suggest a top-down role for action encoding networks in parietal lobe in the evaluation of facial expressions.

Although this study focuses on processing mechanisms specific to faces, the functional interaction of cognitions and emotions may be applicable to more general stimuli.

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