Enter feelings: Somatosensory responses following early stages of visual induction of emotion

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Abstract

In a MEG experiment, we imaged the early dynamics of the human cerebral cortex during the induction of emotion by visual stimuli. We tested the hypothesis that early cortical responses would correlate with the emotional competence of visual stimuli and subsequent subjective ratings of feeling in a set of specific target regions important for somatosensory, attentional, and motivational functions, just after initial visual and appraisal related cortical responses to picture presentation. Relative to the neutral condition, cortical responses, during the 350–500 ms phase of the MEG evoked response, were stronger for both pleasant and unpleasant stimuli in the orbitofrontal cortex, ventromedial prefrontal cortex, anterior cingulate and somatosensory cortices. These responses, which correlated with subjective ratings of arousal, emerged after an initial spreading of cortical activity from early visual cortex (70–200 ms) to the ventral visual stream, temporopolar and orbitofrontal regions (200–350 ms), higher for emotionally competent stimuli than for neutral in the 200–350 ms window, in a manner compatible with an appraisal function. Heart beats occurring during the first 500 ms post stimulus showed longer intervals for unpleasant than for neutral stimuli relative to the preceding beat. The results support the hypothesis of a sequence of processing regarding the emergence of feelings and suggest that, even in the early phase of feeling induction, actual body responses to the inducing stimuli could be represented in the brain.

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1. Introduction

The induction of emotion and feeling by emotionally competent stimuli has been hypothesized to encompass a sequence of stages (Damasio, 1999). In the case of visual stimuli, the following putative stages would occur:

1. Activity propagates from early visual cortices to the dorsal and ventral visual streams, in lateral occipito-parietal and inferotemporal cortices, respectively.
2. Signals from the ventral visual stream, and perhaps from more direct cortical–cortical and subcortical pathways (Catani et al., 2002; Liddell et al., 2005; Rudrauf et al., 2008), reach anterior integrative structures, including the amygdala, the temporal pole (TP), the orbitofrontal cortex (OFC) and the ventromedial prefrontal cortex (VMPFC) (Van Essen, 2004), an ensemble of structures we will refer to as the “anterior affective system”. These structures participate in an evaluation of the significance of the stimulus relative to current motivational state and memory (Damasio, 1994; Kringelbach and Rolls, 2004; LeDoux, 1998; Rolls, 2000). They also trigger and control further emotional responses based on this evaluation, including: a tuning of attention within the relevant modality, putatively occurring via backward projections (Rudrauf et al., 2008), an increase in central and peripheral arousal, and the triggering of valenced visceral and musculo-skeletal motor programs, under the control of the basal ganglia, hypothalamus and brainstem nuclei (Carmichael and Price, 1995; Kringelbach and Rolls, 2004; LeDoux, 1998; Rolls, 2000).
3. The process of feeling emotion is hypothesized to begin just after the onset of these emotional responses (Damasio, 2003), which include central and peripheral components. Emotional feelings

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1 “Emotional competence” is an expression that is often used by Antonio Damasio to designate the property that stimuli can have of inducing emotions in subjects. This property can be related to the nature of the stimulus, and/or the (possibly acquired) dispositions of a subject to respond to this stimulus.
include a subjective experience of increased central and peripheral arousal, eventually valenced by the motivational aspects of the affective response (Bradley et al., 2001; Russell and Barrett, 1999). We see feeling as resulting in part from the monitoring and control of the “upheaval” caused by the unfolding emotional state (Rudrauf and Damasio, 2005), specifically from: (a) motivational systems controlling the emotional response (including the amygdala, OFC and VMPFC); (b) somatosensory mapping of the induced emotional state (occurring in somatosensory regions including the somatosensory cortices); and (c) attentional and executive mechanisms integrating the newly developing state and reacting to it (involving the ACC). In fMRI studies, the OFC and VMPFC have been shown to be active during various feeling states in response to primary, secondary, concrete and abstract rewards (see Kringlebach and Rolls, 2004). The involvement of somatosensory cortices in feeling emotion (SI, SII, and the insula) is supported by several human experimental studies using structural and functional neuroimaging, as well as other electrophysiological methods (Craig, 2002; Critchley et al., 2002a; Damasio et al., 2000; Lane et al., 1997b; Phillips et al., 1997; Reiman et al., 1997; but see Rolls et al., 2003). The ACC, along with more anterior medial prefrontal cortices (Bermohi et al., 2006), has been shown to play an important role in arousal, attention, motivation, emotion and feeling (Bush et al., 2000; Lane et al., 1997a; Stoleru et al., 1999), in the sense of self (Damasio, 1994, 1999; Northoff et al., 2006), in the interaction between emotion and attention (Fichtenholtz et al., 2004; Yamasaki et al., 2002), in the top-down modulation of intense emotional responses (Beauregard et al., 2001; Phan et al., 2004), and more generally in awareness (see Mayr, 2004). These structures can operate together during the processing relevant to emotional feeling (Critchley et al., 2000, 2002b, 2003).

Growing empirical evidence supports the importance of somatosensory processes in emotional feeling. However, there is still some skepticism regarding whether such processes could rely on actual sensory feedback from the body proper, one counter argument being that the “body-loop” would be too slow to support prompt feeling. An alternative or parallel mechanism has been hypothesized, the “as-if body-loop”, involving the simulation and/or reactivation of memorized somatosensory patterns of emotion (see Damasio, 1994). The fact that there are strong bidirectional connections between the anterior affective system and somatosensory and viscerosensory structures is compatible with the “as-if body-loop” hypothesis (Mesulam and Mufson, 1982; Mufson and Mesulam, 1982). Moreover, the discovery of mirror neurons (Rizzolatti et al., 1996) provides indirect evidence for an “as-if” principle because when mirror neurons execute a simulation of the body states of others, they must rely on the prior simulation of the subjects' own body state.

Here, we wanted to test our hypothesis regarding the chronology and functional neuroanatomical basis of the feeling process. To support the hypothesis, we should be able to show, using time sensitive brain imaging approaches, that concurrent activity in SI, SII, the insula, OFC, VMPFC, MPFC and ACC, correlates with the emotional competence of the stimuli and subsequent subjective ratings of feeling, shortly after evidence of visual processing along the ventral visual stream (mesial occipital, ventral occipito-temporal and infero-temporal cortex), and initial responses in appraisal related cortices (the TP, OFC and VMPFC). We also wanted to investigate, although in a more limited manner, whether actual bodily responses correlated with emotional competence would be present before or during the initial somatosensory response that we hypothesized in stage 3. This would suggest a possible engagement of a classical body-loop even in the earliest phase of the feeling process. Alternatively, if putative somatosensory responses correlated with feeling occur without evidence of parallel actual body responses, this would suggest the involvement of an as-if body loop mechanism.

In order to test for early bodily effects, we examined the early heart rate responses to the stimuli (the main psychophysiological parameter that we could collect in a MEG environment using an EKG). The typical cardiac response to stimuli includes an initial deceleration, followed by a relative acceleration and another deceleration, all occurring within the first few seconds after stimulus presentation (see Graham, 1978, 1979). Emotionally competent stimuli tend to induce, among other effects, stronger initial deceleration compared to neutral stimuli, most reliably and strongly in response to unpleasant stimuli (even though the literature is not fully consistent on this matter; Bradley et al., 2001). Because we wanted to examine the earliest cardiac responses, we had to use a method resulting in low statistical power, as it involved nonoptimal sampling (see Section 2.6). We thus decided to only test for the significance of the effects that were expected to be strongest: the differential heart rate deceleration in response to unpleasant versus neutral stimuli.

A specific time window of interest was defined in order to operationalize our hypotheses, focusing on the earliest stages of emotion induction. The completion of stages 1 and 2 (initial sensory, evaluative and emotion triggering processing), and the initiation of stage 3 (feeling), was expected very early after stimulus presentation. Electrophysiological studies demonstrate that initial visual processing in the human cortex starts as soon as 50–70 ms after stimulus presentation for primary visual response (Moradi et al., 2003), and that the first stages of appraisal of visual stimuli in the anterior affective system, i.e. the evaluation of the emotional significance of the stimuli, start as early as 120–180 ms (Eimer and Holmes, 2002; Kawasaki et al., 2001; Pizzagalli et al., 2002; Streit et al., 2003). Amplitudes of event-related potentials (ERPs) show correlations with ratings of pictures for arousal as early as 300 ms post-stimulus onset (Bradley and Lang, 2000). Importantly, modulation of peripheral nervous system activity can appear quite early too. Nonspecific changes in muscular tone in response to pictures are observed as early as 200 ms post-stimulus onset (Dimberg and Pettersson, 2000). Modulation by emotional competence in the corrugator muscles, well established just after 500 ms, could begin between 350–500 ms after stimulus presentation (Dimberg and Pettersson, 2000). Though some caution is warranted when interpreting studies not designed to specifically test these early effects, there is a suggestion that heart rate may be modulated by emotional competence in response to emotional stimuli as early as during the first 500 ms of stimulation (Bradley et al., 2001; Buchanan et al., 2006). Following visual and evaluative processing, the early stages of feeling can be expected to begin within 300–600 ms after presentation of the stimuli. This is a time window of high signal to noise ratio for many ERPs or their magnetoencephalographic (MEG) equivalent, the event-related fields (ERF).

In order to test our hypotheses, we used magnetoencephalography (MEG) with distributed source reconstruction (Baillet et al., 2001; Dale and Sereno, 1993; Hamalainen et al., 1993), along with analysis of heart beat modulation, in subjects presented with emotionally competent dynamic visual stimuli. The emotional competence of the stimuli, defined as the ability of the stimuli to induce emotional responses, was indexed by EKG parameters and subjective ratings of arousal and valence. The results are in general agreement with the hypotheses.

2. Materials and methods

2.1. Subjects

Fifteen normal right-handed male volunteers, mean age 26 (20–45), participated in the experiment. Subjects had no history of neurological or psychiatric disease and had normal or corrected-to-normal vision. All the subjects gave written consent to participate in the study and were paid for their time. The design and procedures of the experiment were approved by the French national ethical committee.
2.2. Stimuli and procedure

Sixty pleasant, 60 unpleasant and 60 neutral movies depicting complex visual scenes, each with a duration of 10 s, were presented in random order on a screen placed in front of the subjects in the MEG shielded room. We chose the classes of stimuli for the pleasant and unpleasant conditions that elicit the strongest and most reliable emotional responses in normal adult male subjects (Bradley et al., 2001). These classes of stimuli have also been found to be involved in early emotional modulation of visual attention (Anderson, 2005). The pleasant movies depicted erotic content, the unpleasant movies depicted fearful or disgusting content, and the neutral movies included natural scenes, landscapes, neutral faces, and objects.

Each movie panned across a static color photograph in a smooth and continuous manner (e.g., as in close-up footage from a camera panning slowly across a painting). The movie window was centered on the presentation screen and encompassed approximately 10° of visual angle (larger aspect; aspect ratio height/width = 0.79). The amount of displacement of the camera along the background static picture was overall counterbalanced across conditions: there was no significant difference across conditions in the frequency at which the center of the “camera” fell within any of the four quadrants of the underlying static picture ($\chi^2(3)=3.26; p=0.35$). Each movie was built using Matlab (The Mathworks, Natick, MA). Brightness and contrast were normalized by equalizing image histograms using Matlab scripts. The frame rate was 30 fps.

The movies were designed so that they would start with frames which unambiguously conveyed the emotional content of the whole sequence (e.g. if the movie panned along a mutilated body, the initial field of view clearly depicted a mutilated body). The amount of displacement of the camera during each movie was voluntarily kept small. In general, most of the salient/central/meaningful elements of the underlying picture were always apparent in the field of view, and the most salient information was never fully outside of the field of view. This design was aimed at limiting the effect of anticipation/surprise for elements which came into view from outside of the initial field of view, and subjects were made aware of this feature. The experiment was designed in order to be able to study both: (1) early processing in response to movie onset (during the 800 ms of the time window which constitutes the bulk of the evoked response, and which is the focus of this report because of the hypothesis tested); and (2) processing involving a longer time scale, with a special interest in the dynamics of emotional experience, for which the use of movies was critical, but which is beyond the scope of the current article (see Supplementary material online for information about the other subjective ratings).

The onset of the next trial started 2 s after completion of the ratings. The total rating time after each movie presentation was variable with a duration of at least 30 s, thus giving a substantial amount of time for the emotional state to subside (see Garrett and Maddock, 2001). The 180 trials were distributed into 12 runs of 15 trials each. All stimuli and scales were presented on a screen in the MEG shielded room with a video-projector outside of the room, via a series of lenses and mirrors.

2.3. Recordings

The subjects were tested at the Paris MEG facility (http://web.ccr.jussieu.fr/meg-center/; UPMC, CNRS, INSERM, CEA, Hôpital de la Pitié-Salpêtrière), using a 151-axial-gradiometer whole-head MEG array CTF Omega system (VSM MedTech Ltd., Coquitlam, BC, Canada). MEG data sampling frequency was 625 Hz, and acquisition high-pass filter threshold 0.65 Hz. Before each acquisition run, the position of the subject’s head was located using three fiducial coils placed next to the left and right ears and on the nasion.

An electrocardiogram (EKG) was recorded using two silver chloride electrodes, one at the bottom of the neck on the right, the other on the left lateral costal margin. For artifact correction purposes, vertical and horizontal electro-oculograms (EOG) were recorded using pairs of silver chloride differential electrodes with bitemporal and suboccular-frontal placements respectively.

T1-weighted MRIs of the subjects’ brains were acquired at the Centre de Neuroradiologie of the Hôpital de la Pitié-Salpêtrière using a 1.5 T GE Signa scanner with a sagittal acquisition (3D SPGR TR=24 ms TE=8 ms; 124 1.3 mm joint slices, 256×256; FOV=25 cm). Fiducial markers clearly visible on MRI images were placed at the same locations as the fiducial coils during MEG recording in order to facilitate coregistration between the MRI and MEG reference systems.

2.4. Artifact correction and basic post processing

Ocular and cardiac artifacts were removed from the MEG data. Blinks were visually identified on the MEG signal with the help of the EOG, and a window was manually defined around the blinks in order to define their onset and offset. A Savitsky–Golay filter was used in order to fit polynomials on the blink waveforms within the windows of interest. The blinks were then removed from the signal by local linear decorrelation. Cardiac artifacts were detected using the EKG as a temporal reference. MEG signals were averaged around the EKG r component for each MEG channel independently, in order to extract the typical artifact cardiac waveform associated with a given channel, within a given run and a given subject. The channel-specific cardiac waveform was then fitted to each individual cardiac artifact and subtracted from the MEG signals. MEG signals were corrected for inter-run head movements using procedure implemented in the BrainStorm toolbox for Matlab (http://neuroimage.usc.edu/brainstorm).
2.5. EKG processing targeting early effects

R–R intervals have an average duration of about 1 s but a subsecond resolution for heart rate modulation can be achieved with proper averaging techniques over multiple trials. Heart rate was extracted from the EKGS using an inhouse Matlab program. EKGS were corrected for linear trends (anchor points every two and a half seconds). The square of the derivative of the signal was thresholded above two standard deviations in order to identify windows of occurrence of the R waves. The maxima of the detrended EKG within these windows were used to identify the peaks of the R waves. All the trials for all the subjects were visually checked for correct detection of the peaks. The inverse of the inter–peak intervals was computed and expressed in beat per minute (b.p.m) providing a measure of heart rate.

We did not use standard interpolation techniques attributing heart rate values associated with a given R–R interval to every data point in the full interval (Bradley et al., 2001; Buchanan et al., 2006). These techniques, although increasing statistical power, can artificially lead to retrospective attribution of modulatory effects induced by stimulus presentation, on heart rate measured at time points corresponding to the beginning of the interval, while in fact the triggering of the modulation takes place during its latest part. We thus associated the calculated heart rates with the time points corresponding to the second beat (see also Graham, 1978). Such an approach reduces drastically the statistical power of the analysis because not all trials will show beats at any given time instant. Thus in order to limit this inevitable reduction of power, we averaged the local measures of heart rate through time bins of 500 ms, aligned with stimulus onset. 500 ms corresponded to the longest time bin possible given the time interval relevant for our hypothesis. Our approach is conservative as it guarantees that an actual peripheral effect, i.e. the occurrence of a beat with a modulated latency due to stimulus presentation, has indeed taken place within the time bin it is measured. Average values of heart rate in the two bins prior to stimulus presentation were subtracted from the post stimulus heart rate measures in order to obtain a measure of heart rate change (Bradley et al., 2001).

2.6. MRI post processing and coregistration

The subjects' T1 weighted MRIs were processed for extraction of the individual cortical surfaces, using BrainVisa (http://brainvisa.info/), except for 2 brains that had been previously processed with FreeSurfer (http://surfer.nmr.mgh.harvard.edu/). Following automatic tissue segmentation, each brain's cortical surface (grey/pial interface) was subsequently triangulated. The resulting dense tessellations were reduced to approximately 10,000 vertices for subsequent estimation of the local cortical currents. In the perspective of computing relevant group statistics across the individual activation patterns, spatial normalization for the individual tessellations was achieved following a procedure of landmark-based pseudo elastic warping derived from Drury et al. (1996) and Fischl et al. (1999). 36 anatomical landmarks, consisting of points defined along major sulci and gyri, were manually delineated on each hemisphere for every subject's brain. After projection into Talairach's reference system, each hemisphere was inflated to a sphere. Landmarks of each individual brain were moved toward homologous landmarks from a reference brain (here one brain from the cohort of subjects). The displacement of the landmarks generated pseudo body forces, inducing tension in the network and driving the displacement of the other vertices. Registration was achieved when the derivative of the displacement field was below a certain threshold.

2.7. MEG processing and source reconstruction

In order to test our hypothesis, and because our primary interest was on the sequencing and timing of responses over large areas of the cerebral cortex, we used MEG with cortically constrained distributed source reconstruction (Baillet et al., 2001; Dale and Sereno, 1993; Hämäläinen et al., 1993). In spite of its limited localization ability, MEG is the only tool available to date, perhaps along with high density EEG, capable of providing an estimate of the macroscopic aspects of the whole human cerebral cortex electrical dynamics at the time scale of neuronal activity. This approach had the limitation that it excluded subcortical structures from the analysis, such as the amygdaloid complex. Although such structures are fundamental for emotion, our hypothesis mainly concerned cortical areas, so that this strategy of analysis was well suited to test it.

We used event-related response averaging for the analysis of the data, which is generally more straightforward and provide better signal-to-noise ratio than single trial analysis. One limitation of evoked responses is that they tend to open a reliable window on brain activity only for a few hundreds millisecond after stimulus onset (the average signal decaying rapidly), and reflect only very stereotyped and reproducible events. For the purpose of this study, this short time window appeared sufficient because our hypothesis regarded responses expected to start shortly after the earliest stages of processing of the stimuli during the first 500–600 ms after stimulus presentation (see Introduction). Moreover, because we used stereotypic and emotionally potent stimuli, the early brain responses and earliest phases of feeling induction were expected to be rather systematic and stereotyped. This would not be the case for later phases of feeling unfolding, which continues far beyond the limits of the time window of interest, and becomes more unpredictable as time goes on.

Based on these principles, artifact corrected MEG signals were averaged across trials within each experimental condition (neutral, pleasant, unpleasant stimuli), taking movie onset as temporal reference. The forward and inverse source imaging problems were solved using anatomical priors based on the assumption that the main contributions to the MEG signals originate from cortical currents oriented perpendicularly to the cortical surface (Baillet et al., 2001; Hämäläinen et al., 1993). The head volume conductor was modeled with three concentric spherical shells, which in MEG versus EEG provides a sufficiently accurate approximation (Darvas et al., 2004; Leahy et al., 1998; Yvert et al., 1997). Elementary current dipole sources were distributed at the nodes of each individual cortical envelope, normal to the cortical surfaces. A gain matrix was computed for each subject and each condition using the quasi-static approximation of Maxwell's equations, using procedures implemented in the BrainStorm toolbox for Matlab (http://neuroimage.usc.edu/brainstorm). The time courses of the current-dipole moments over the cortical surface were estimated using Tikhonov-regularized weighted linear minimum-norm solutions to the inverse problem, also from Brainstorm (Baillet et al., 2001; Dale and Sereno, 1993). The Tikhonov regularized weighted minimum-norm approach provides an optimal solution when a minimum of a priori information has to be used: it gives the solution J\* (the estimated distribution of current densities) which corresponds to the distribution of current densities with the maximum likelihood, max(p(J|M)), given, M, the measured MEG signal, the equations of electromagnetism, the possible space of sources, and assumptions on the noise (see Baillet et al., 2001). We used the same adaptive values for the Tikhonov regularization parameter across all datasets, that is: 10% of the maximum singular value of the associated lead-field matrix. The weighted minimum-norm involves a reweighting of the gain matrix, aimed at compensating for known bias favoring proximal sources in the original method. For each dipole, the modulus of the current-dipole moment was noise normalized through a Z-score procedure using a 500 ms baseline before stimulus onset, providing a measure of normalized dipole strength.

2.8. Statistical analyses

The general linear model (Myers, 1990) was used in order to compute Statistical Parametric Maps (SPMs), implementing one-way ANOVAs for repeated measure designs and testing for one-tail specific
contrasts such as pleasant minus neutral (P−N) and unpleasant minus neutral (U−N) stimuli, based on an hypothesis of higher activity in response to emotional versus neutral stimuli. We thresholded our SPMs not only based on the p-values but also on the spatial extent of the activated vertices (i.e. vertices associated with effects reaching the uncorrected threshold of p<0.05). Only activated vertices belonging to clusters of at least 100 adjacent activated vertices were conserved. We choose 100 vertices because, on average, this encompassed approximately half of the cortical surface covered by each region of interest (ROI) (see Table 1 and Fig. 2B), so that sub-ROI resolution could still be achieved. On average, 100 activated vertices corresponded to a mean cortical surface size of about 9 cm², with 6.9 cm² standard deviation (across all vertices and for random patches of 100 connected vertices on the reference brain). The mean cortical surface per ROI was about 19.8 cm² (approx. 194 vertices on average), with 9.7 cm² standard deviation (approx. corresponding to 98 vertices). No further assumption was made about the shape of the clusters because of the high variability in shape of anatomical-functional cortical areas, which, as suggested by Brodmann’s cytoarchitectural parcellation, led to the expectation of oblong (e.g. BA 1,2,3) as well as square-like (e.g. BA 40) possible activations if specific anatomic-functional areas were fully activated.

As were primarily interested in the effect of emotional competence be it pleasantly or unpleasantly valenced, conjunction maps were generated, showing where effects of cortical activations were significant for both for P−N and U−N contrasts. We chose this approach rather than averaging together data for pleasant and unpleasant stimuli prior to source reconstruction, in order to avoid the possibility of one type of emotional stimulus driving the observed effects. Effects had to appear in both type of stimuli and thus to be confirmed in two independent conditions/datasets.

In order to test for the presence of correlations between brain signals and subjective ratings, we used a ROI approach. Six ROIs relevant to our hypothesis regarding feeling were selected: the OFC, VMPFC, ACC, INS, SI and SII (see Table 1 and Fig. 2B). The initial set of ROIs was chosen based on their relevance for the stimuli, tasks and modality of stimulation, involving visual processing of emotionally competent stimuli. ROIs were defined based on anatomic-functional criteria, and were partially informed by the apparent signal propaga-
The hypothesis of an early modulation of heart rate by emotional competence during the time window of interest, at least for unpleasant stimuli, was supported. Specifically, there was more deceleration during the first 500 ms after stimulus onset for unpleasant than neutral stimuli (one-tailed t-test for paired samples, \( t(14) = 1.86; p < 0.05 \)).

3.2. General pattern of cortical response

Fig. 1 shows cortical maps of the grand average of the source reconstruction results for pleasant stimuli for successive time instants (the observed pattern of activation is very similar for all three conditions). Three main time periods can be distinguished. T1 (from 70 ms to 170 ms): responses three standard deviations above baseline were first observed in the primary visual cortex (starting around 70 ms), followed by activity spreading (100 to 170 ms) over the rest of the occipital cortex. There were indications of early responses in the OFC and TP during this period (see Rudrauf et al. 2008 for a detailed analysis of the dynamics of such early responses). T2 (from 200 to 350 ms): after a brief and widespread drop in activity (between 170 and 200 ms), activity propagated slowly from the occipital cortex along areas corresponding to the ventral visual stream (ventral occipito-temporal cortex, ventral and lateral infero temporal cortex), terminating with increased signal in the temporal pole (TP). T3 (from 350 to 500 ms), an extensive increase of activity appeared in the OFC, lateral temporal cortex (LTC), the frontal and parietal opercula (including part of SII) and the dorsal ACC.

3.3. Effects of emotional competence on the cortical response

Fig. 2A presents SPMs resulting from the conjunction analysis, showing areas of overlap between effects significant for both the pleasant minus neutral (P−N) and unpleasant minus neutral (U−N) contrast. We emphasized results for the time period of interest at the end of the evoked response (T3), when responses related to initiation of feeling were expected. Successive views of the SPMs for the contrast (P−N) are also shown.

During T1, early significant effects (100–160 ms) with greater activations for pleasant than for neutral stimuli (P−N) were found in the TP and OFC, as well as in inferotemporal and insular regions, but not with the contrast U−N, thus the conjunction maps do not show effects during this time period. During T2 (200–350 ms), most of the cortices corresponding to the ventral visual stream, as well as the TP and OFC, showed sustained significant effects both for (P−N) and (U−N) (Fig. 2A). Effects also appeared both for (P−N) and (U−N) in the dorsal cingulate. During T3, significant effects were observed in the OFC, VMPFC, dorsal and perigenual ACC, right SI and SII and left insula, both for (P−N) and (U−N). Effects only significant with (P−N) included the left dorsolateral prefrontal cortex and lateral and infero temporal cortices bilaterally. With (P−N) right somatosensory and somatomotor cortices, including all SI and SII, were fully covered by significant effects, while neither adjacent post central sulcus or middle prefrontal gyrus showed significant effects.
Of note, effects for \((P - N)\) were generally larger, more significant and spatially more extended than those for \((U - N)\), in agreement with the observation that the pleasant stimuli had, on average, more emotional competence than the unpleasant ones.

3.4. Correlations with subjective ratings

Fig. 3 presents the results of the correlation analysis for arousal in the regions hypothesized to be relevant for feeling \((SI, SII, insula, OFC, VMPFC and ACC)\). There were no significant correlations with valence in the time window analyzed. Overall, the level of correlation between arousal and the activations in most of these ROIs shows a bilateral pattern of progressive increase, from the beginning of the evoked response \((70–200\, ms)\) until the late part of the response \((350–500\, ms)\) corresponding to \(T3\). The insula, however, showed a rather stationary level of correlation after an initial increase. In all the ROIs but the insula, the correlations reached the threshold of significance during \(T3\), at least in one hemisphere. These significant correlations were observed at the level of somatosensory cortices \((SI and SII)\) on the right hemisphere, and on the left hemisphere for SI. Correlations were significant during \(T3\) in the OFC, VMPFC and ACC on the left hemisphere only, but the level of correlation in these three regions on the right hemisphere crossed the threshold corresponding to an uncorrected \(p < 0.05\) during the same period.

4. Discussion

This study focused on the involvement of specific cortical regions in the induction of feeling, namely SI, SII, the insula, the OFC, VMPFC and the ACC, the activation of which was expected to take place after initial sensory and appraisal stages. We selected a time window of activation based on theoretical rationale and empirical evidence regarding the chronology and chronometry of these processes. Our source reconstruction analyses revealed activity in the regions of interest, higher for both pleasant and unpleasant stimuli than for neutral. The activities, occurring during the late phase of the MEG evoked response \((350–500\, ms)\) were largely correlated in the ROIs with subsequent subjective ratings of arousal. These effects appeared after evidence of initial processing of the stimuli in visual occipital areas \((70–200\, ms)\), followed by responses in ventral visual stream areas \((200–350\, ms)\),
Fig. 3. Correlation of cortical activity in ROIs with arousal. The graphs represent the $t$ values associated with the regression analysis assessing the level of correlation between arousal rating and cortical activity (see Method section), for the six successive time instants, for the ROIs belonging to the hypothesized network (see text). The inferior horizontal line represents the uncorrected threshold of $p < 0.05$. The superior line represents the corrected threshold. The gray column corresponds to the time window of interest for our hypothesis.
along with responses in the TP and OFC (100–350 ms). The latter responses are compatible with initial appraisal and emotion triggering stages predicted by our model, also indirectly supported, in a more limited manner, by the presence, at least for unpleasant stimuli, of actual body responses in the first 500 ms after stimulus onset indexed by heart rate deceleration. The results thus support the hypotheses.

A study using distributed source reconstruction on low-density EEG recorded during presentation of faces with various facial expressions showed effects of emotional facial expressions in the temporal and orbitofrontal cortex (Esslen et al., 2004), but did not report effects in somatosensory cortices. Although one might note that the use of low-density EEG might have limited the source reconstruction procedure, it is more likely that the absence of effects in that study was due to the use of faces, which are not the most potent stimuli for induction of overt emotional responses and are more effective in recognition paradigms. This lack of an effect for faces alone also supports the idea that the effects observed in our experiment are likely to be mainly due to processes related to emotion induction rather than emotion recognition. Our study did not particularly require emotion “recognition”, since the stimuli used did not display systematic emotional expressions to be recognized. We used stimuli which have been demonstrated in the literature and in our subjects to induce strong emotional responses. Another study used minimum norm source reconstruction on high-density EEG with stimuli that were similar in content to those we used in our study. That study showed effects of arousal on early (N1) and later (including the P300) components of the response (Keil et al., 2003), but the sources were reconstructed on simple embedded spheres which could not provide a satisfactory localization of the generators.

A more recent study recording high-density EEG during emotional picture presentation used a heartbeat perception task to separate subjects into groups with either higher or lower interoceptive awareness (Pollatos et al., 2007). The results showed a positive correlation between interoceptive awareness performance and the experienced intensity of emotions, with a P300 amplitude to pleasant and unpleasant pictures of higher magnitude for subjects with high interoceptive awareness. Source reconstruction of the P300 component, contrasting subjects with higher versus lower interoceptive awareness performance, suggested more involvement of the insula, somatosensory cortices, anterior cingulate, and prefrontal cortices, in subjects with higher interoceptive awareness performance than in subjects with lower interoceptive awareness performance during emotional picture presentation. This study, although not specifically interested in the chronological sequence of activation related to the emergence of feeling, shows findings compatible with our general theoretical framework.

The presence in our study of early body responses to emotional stimuli is compatible with the hypothesis that the reconstructed somatosensory effects could reflect sensory representation of feedback from the body, even at the earliest phase of feeling. The conclusions that can be drawn from our results are very limited, as we only tested effects for the unpleasant – neutral contrast in heart rate deceleration. We did so because of the well documented pattern of response during the first phase of the heart rate response to picture presentation (Bradley et al., 2001). Also our statistical power was very limited due to the use of a method specifically developed to target early effects (see Methods). Of note partial evidence of early effects of bodily responses to emotional stimuli have also been suggested elsewhere (Bradley et al., 2001; Buchanan et al., 2006; Dimberg and Petterson, 2000). If such effects would be fully confirmed, although the parallel involvement of an “as-if-body loop” mechanism could not be ruled out, it would not seem necessary as a replacement for actual body responses, even for the earliest phase of the emergence of feeling. It is still plausible that the observed somatosensory modulation might reflect a combination of an early feedback from the body, an “attentional” response modulating somatosensory integration, and “simulated” proprioceptive and interoceptive components.

We found more effects in SI and SII than in the insula, especially in the correlation with arousal. This could be due to the fact that the insula is a deep cortical structure whose activity might be less reliably detected by MEG and source reconstruction methods than the activity of superficial regions such as SI and SII, known to be well detected by MEG. Another explanation would be that, at least in this early phase of feeling induction, the somatosensory representations of musculoskeletal and tegumental changes might play a more prominent role than the interoceptive representations of visceral changes. Although visceral perception is a prominent component of the phenomenology of feeling, we believe that musculoskeletal and tegumental sensations are also important. Moreover, it is likely that an important part of the conscious visceral sensations involved in feeling emotions, such as cardiovascular and respiratory sensations, are in fact indirect and mediated by interactions with skin and striated muscles. The skin provides an important interface of sensory transduction, in terms of both thermoreception and mechanoreception, for changes relevant to emotion in adjacent visceral systems (blood pressure, cardiac pulsations, blood volume shifts from superficial to deeper skin layers, as well as sweating and respiratory amplitude and frequency).

Given the latencies of the body responses involved in the time window of interest, it is unlikely that their neurophysiological control is mediated by sympathetic influences, which are notoriously slow. However, vagal parasympathetic influences, the modulation of which can lead either to decrease or increase of autonomic tone, can be extremely fast. Although the question of how early these heart beat effects might begin has not been addressed specifically before, heart rate deceleration induced by unpleasant and pleasant visual stimuli is presumed to occur under parasympathetic influence (Bradley et al., 2001). Incidentally, we should note that a slowing down of visceral functions does not imply that the correlated somatosensory representations should consist of deactivations rather than activations. Sensory systems can respond to such peripheral changes with either activations or deactivations.

The decrease of heart rate, correlated with arousal after perception of visual stimuli, has been interpreted as part of an initial orienting response (Graham, 1979; Bradley et al., 2001). The notion of an orienting response tends to be associated with that of attention, as opposed to emotion, but we want to emphasize that the type of orienting responses involved here should be appropriately considered emotional because it includes, within the same time window, emotional appraisal and motivation, bodily responses, arousing of somatosensory monitoring, as well as attentional and executive reactions. Based on these considerations, it is plausible that the brain responses observed in our study during the last part of the evoked response reflect the rise of an early monitoring process associated with perceiving an early and general stage of emotional “upheaval”.

The effects found in the ACC, a structure known to be involved in attention and executive responses in interaction with emotion, are compatible with this idea. Such an interpretation might however be questioned given that several results suggest (see notably Phan et al., 2002) that the ACC appears to be activated in emotion-related protocols more often when especially intense feelings are experienced (suggesting that the ACC is called to act when there is a need for control), or when the task explicitly involves either attentional demand, monitoring feelings or retrieval of emotional memory. Our study did require monitoring feeling in order to produce subjective ratings, and involved intense emotions. This situation might lead to a potential confound regarding the interpretation of the responses reconstructed in the ACC. Nonetheless, it can be argued that, in our experiment, the task of monitoring feeling, which requires sustained attention to one’s own body state, was enhanced for all categories of stimuli, neutral, pleasant and unpleasant, and that the subjects could not predict the category of stimulus they would be presented with. As
a result, the differences between emotional and neutral stimuli might not be simply explainable in terms of a general and non-specific difference in attention. Our theoretical framework implies that feelings depend on interactions between somatosensory, attentional and executive processes, in the context of an emotional upheaval requiring monitoring and control. The framework predicts that as more attention is recruited toward somatosensory information, and as the system reacts to its own perturbed state more strongly, the intensity of feeling should be augmented. In other words, we should not consider the combination of increased attention and of increased call for control as a confound. Both of these neurocognitive factors are contributors to the feeling process itself, and will thus necessarily correlate with feeling. Of note, increased feeling intensity with increased attention toward emotional information has been demonstrated (Bermpohl et al., 2006), although the neural correlates were found in MPFC rather than in the ACC itself. Even so, there are indications that attentional and executive frontal mesial networks are involved in the perception of feeling intensity, even if these networks are not always significantly activated during emotion processing.

In our study, we found significant correlations of activity in somatosensory cortices with subjective ratings only for arousal and not valence. The prevalence of a correlation of the early brain responses with arousal has been suggested by classical results in scalp EEG, which found a linear relationship between arousal and the scalp positive potential Pz starting at around 200–300 ms (Cuthbert et al., 2000). This is compatible with our interpretation of the results in term of the rise of an early monitoring process, associated with perceiving an early stage of emotional upheaval. More complex and differentiated feelings would occur later.

We focused on the earliest stages of the emotion induction, as a strategy of analysis related to chronological and chronometric hypotheses, allowing for the definition of a precise time window of interest, and the correlative use of a method based on evoked responses favoring high signal-to-noise ratio. Unfortunately, in general, this method is not conducive to investigating the neural dynamics beyond a few hundred milliseconds after stimulus onset, except for specific late potentials. Although the focus on those earliest stages was sufficient to test our general hypothesis, it imposed a significant limitation both in our ability to comprehensively investigate the neural correlates of feeling, and to use subjective ratings to their fullest extent. The subjective ratings we obtained referred to an experience of several seconds, that is, to an experience that would have begun during the first 500 ms of the response but would have continued beyond that period. In other words, the segment of brain activity analyzed here cannot be perfectly correlated with the whole set of subjective phenomena expressed in the rating. It is reasonable to assume, however, that the processes unfolding during the time window of interest, especially those corresponding to the late components of the evoked response (between 350 and 500 ms), would have contributed significantly to the overall subjective experience expressed in the ratings. This is particularly true for the type of stimuli we used, which tend to induce strong and rather stereotypic emotional responses. In subsequent studies we plan to use more advanced approaches to signal analysis in order to characterize brain activity during the phase of clear correlation between heart rate change and valence around 4 s after stimulus onset. The curve of correlation between heart rate change and valence itself could be used to search for corresponding covarying activity in the brain in order to reveal important aspects of the brain basis of valenced feeling.

More generally, it is important to note that “subjective ratings” are only indirect measures of actual “subjective states”. Instructions, feedback, demographics, unconscious psychological factors, social norms, etc. can impact ratings, and although we tried to obtain the most faithful ratings possible by working with the subjects during training sessions, it is important to acknowledge that using subjective ratings to index subjective states involves a layer of inference. In conclusion, we provide support for the hypothesis that a network of cortical areas involved in motivation, somatosensing, attention and executive control is involved in the early emergence of feeling emotion induced by presentation of emotionally competent visual stimuli. This network was active at the same time as body responses correlated with emotional competence. The effects were not specific to valence, and were observed for both pleasant and unpleasant stimuli. The effects regard arousal of somatosensory and attentional responses, in the context of a probable modulation of body responses taking place during the initial orienting part of emotion induction.

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