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Emotion and attention interactions in social cognition: Brain regions involved in processing anger prosody

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Multiple levels of processing are thought to be involved in the appraisal of emotionally relevant events, with some processes being engaged relatively independently of attention, whereas other processes may depend on attention and current task goals or context. We conducted an event-related fMRI experiment to examine how processing angry voice prosody, an affectively and socially salient signal, is modulated by voluntary attention. To manipulate attention orthogonally to emotional prosody, we used a dichotic listening paradigm in which meaningless utterances, pronounced with either angry or neutral prosody, were presented simultaneously to both ears on each trial. In two successive blocks, participants selectively attended to either the left or right ear and performed a gender-decision on the voice heard on the target side. Our results revealed a functional dissociation between different brain areas. Whereas the right amygdala and bilateral superior temporal sulcus responded to anger prosody irrespective of whether it was heard from a to-be-attended or to-be-ignored voice, the orbitofrontal cortex and the cuneus in medial occipital cortex showed greater activation to the same emotional stimuli when the angry voice was to-be-attended rather than to-be-ignored. Furthermore, regression analyses revealed a strong correlation between orbitofrontal regions and sensitivity on a behavioral inhibition scale measuring proneness to anxiety reactions. Our results underscore the importance of emotion and attention interactions in social cognition by demonstrating that multiple levels of processing are involved in the appraisal of emotionally relevant cues in voices, and by showing a modulation of some emotional responses by both the current task-demands and individual differences.

Keywords: Emotion; Attention; Appraisal; Prosody; Anger; Amygdala; STS; Orbitofrontal cortex

Introduction

Efficient processing of emotional cues, such as facial and vocal expressions, is critical during social interactions (see Russell et al., 2003; Scherer, 1986, 2003). However, despite a growing interest in this issue in cognitive neuroscience, the neural mechanisms involved in emotional decoding and their interaction with other cognitive processes remain poorly defined (see Goldman and Sekhar Sripada, 2005). Moreover, neuroscience research has often focused on the perception of faces and facial expressions, but questions concerning how emotional signals in the *voice* are processed in the human brain have only rarely been investigated (see Adolphs et al., 2002; Morris et al., 1999; Belin et al., 2004). Here, we report new results from an fMRI study examining brain responses to angry prosody in voices, and the effects of selective attention on such responses, as well as their modulation by individual differences in affective traits.

In social contexts, detecting anger in other individuals is of particular importance, not only in order to achieve successful social interactions, but also to guarantee safety and adjust behavior appropriately (for example, by reacting with fear or submission, see Frijda, 1987). Given the flow of events entering the cognitive system, together with its processing capacity limitations, a critical function shared by both *emotional* and *attentional* processes should be to prioritize the processing of pertinent events, relative to neutral or mundane events, leading to enhanced perceptual analysis, memory, and motor action (see Compton, 2003; Anderson and Phelps, 2001; D'Argembeau and Van der Linden, 2004; Keil et al., 2003; Lewis, in press; Oatley and Johnson-Laird, 1987; Pourtois et al., 2004; Scherer, 2001, 2004; Wells and Matthews, 1994; Whalen, 1998). Therefore, emotional processing of social signals in faces and voices might be intimately linked to attentional mechanisms, requiring swift evaluation of their affective meaning when they are relevant for behavior as well as when they are currently task-irrelevant but potentially significant. Thus, appraisal theories of emotion have proposed that an early

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and critical evaluation process is responsible for detecting the extent to which stimulus events (e.g., anger prosody in voices during social interaction) are relevant for the momentary hierarchy of goals and needs of the individual, possibly leading to an enhancement of processing resources and a modulation of attentional processes towards these events (e.g., Scherer, 2001; Sander et al., 2003; Sander et al., 2005).

One of the first experimental results supporting this proposal was the "own name effect" obtained in a dichotic listening paradigm. Moray (1959) showed that when a participant is presented with his/her own name in the to-be-ignored ear, while performing a primary task on stimuli heard in the other ear, this task-irrelevant but self-relevant information was more likely to be involuntarily processed and influence performance relative to other types of information (see also Compton, 2003; Robinson, 1998). Similarly, a number of recent results suggest that visual events (e.g., facial expressions or affective pictures) with particular emotional relevance can also capture attention more readily than neutral events (e.g., Mack and Rock, 1998; Pourtois et al., 2004; Vuilleumier, 2002; Vuilleumier and Schwartz, 2001a,b), and converging evidence from a variety of paradigms indicate that some appraisals may be performed when emotional events are implicitly processed (see Compton, 2003; Ohman and Mineka, 2001; Robinson, 1998; Winkielman and Berridge, 2004). Importantly, however, multiple levels of processing are likely to be involved in the appraisal of emotional events, with some neural systems being engaged in a rather involuntary and implicit manner, relatively independent of attention, whereas other systems may require attention and more extensive and effortful evaluation within the cognitive system (see Robinson, 1998; Leventhal and Scherer, 1987; Scherer, 1993).

To date, most brain imaging studies on interaction effects between emotion and attention have concerned the visual domain, but little is known about the neural substrates involved in processing emotional signals from auditory stimuli and in particular from the affective prosody in human voices. In line with behavioral results, recent brain imaging data show that the emotional value of visual stimuli can strongly influence neuronal responsiveness in sensory and memory systems (e.g., Armony and Dolan, 2002; Hadjikhani and de Gelder, 2003; Pourtois et al., 2004; see Adolphs, 2004). Thus, faces with fearful expression may not only activate the amygdala, but also produce greater activation of face-selective areas in fusiform cortex (Armony and Dolan, 2002; Vuilleumier et al., 2001, 2004), presumably through direct feedback from the amygdala (Davis and Whalen, 2001; LeDoux, 1996; Vuilleumier et al., 2004). These findings are consistent with the notion that the amygdala may play a critical role in relevance detection (Sander et al., 2003), allowing efficient orienting of processing resources towards salient events. In the visual domain (e.g., for faces), it has been suggested that such emotional modulation of perceptual processing might operate through mechanisms partly independent of fronto-parietal networks mediating voluntary spatial attention (Vuilleumier, 2002; Vuilleumier et al., 2002). However, few imaging studies have examined how emotional or social signals from auditory stimuli might influence perception and attention (e.g., Jäncke et al., 2001; Sander and Scheich, 2001; Grandjean et al., 2005). Moreover, across different modalities, elucidating how attentional control may interact with affective processing might provide important insights on the neural mechanisms of affect regulation and related individual differences.

Co-existing with these neural networks processing emotional signals independently of endogenously-driven attention, other neural networks might differentially respond to emotion as a function of the current task-relevance or selective attention. For instance, although the amygdala and fusiform cortex can activate to fearful faces without selective attention, regions in medial prefrontal cortex and temporal poles show greater responses to task-relevant than task-irrelevant fearful faces (Vuilleumier et al., 2001; see also Pessoa et al., 2002). Similarly, ERP data (Holmes et al., 2003) showed that emotional faces evoke a greater frontal positivity over the scalp when attended, as compared to neutral faces, but not when unattended. In a PET experiment, Lane et al. (1997) found that a region of the anterior cingulate extending to the medial prefrontal cortex was more activated when subjects focused their attention on the valence rather than on the setting (indoors or outdoors) of emotional pictures (see also Gusnard et al., 2001). These data are consistent with the view that the prefrontal cortex may control attention to emotional information (see Bush et al., 2000; Compton, 2003). Thus, at least in the visual domain, some regions in the prefrontal cortex may respond during emotional appraisal only when attention is selectively directed to the emotional events (Vuilleumier et al., 2003). In the auditory domain, a recent study by Mitchell et al. (2003) also showed greater activation of medial frontal gyrus when participants had to judge the emotional prosody of sentences relative to when they judged the verbal semantic content of the same stimuli.

The current study therefore aimed at further investigating the relationship between appraisal of vocal emotional stimuli and voluntarily-directed attention. We conducted an event-related fMRI experiment during which participants were presented with anger and neutral prosody in a dichotic-listening paradigm, allowing us to compare brain responses to angry voices when the voices were to-be-attended and when they were to-be-ignored.

Our first goal was to determine whether the processing of emotional prosody is modulated by endogenously driven spatial attention. We aimed at distinguishing between (i) neural networks responding to emotional events independently of attention, and (ii) neural networks differentially responding to the same emotional events as a function of auditory attention. To manipulate voluntary attention orthogonally to emotional prosody, we used a dichotic listening paradigm in which meaningless utterances, pronounced with either angry or neutral prosody, were presented simultaneously to both ears. Importantly, only the focus of attention, but not the task, varied across the attentional conditions: participants performed a gender decision task on voices heard in one ear, while they had to ignore voices presented on the other side.

The second goal was to determine whether a modulation of sensory processing by human affective signals might exist in the auditory domain, as previously shown in vision (Vuilleumier et al., 2001). Namely, we tested whether emotional prosody might enhance neural activity in auditory cortex, by analogy with enhancement typically observed for emotional faces in fusiform cortex (Vuilleumier et al., 2004). Notably, however, a modulation of neural responses in the auditory cortex has been reported after aversive conditioning in both animals (Armony et al., 1998) and humans (Morris et al., 1998a). Yet, the effect of affective vocal signals such as emotional prosody on sensory processing has not been systematically investigated. Preliminary results concerning such responses in auditory areas, controlled for the acoustic properties associated with angry prosody, are reported elsewhere (Grandjean et al., 2005).

Finally, given recent evidence suggesting that some brain systems may differentially respond to emotional stimuli arising outside the current focus of attention as a function of individuals' levels of anxiety (e.g., Bishop et al., 2004; Etkin et al., 2004), we also examined whether any attentional influences on emotional processing of voices might be related to individual affective traits as assessed by standard motivational and anxiety questionnaires.

Materials and methods

Participants

Fifteen right-handed healthy undergraduate students at the University of Geneva (seven women, mean age = 24.4 ± 4.6 years) with no history of neurological or audiological illness participated to this study. All participants also filled in the STAI questionnaire (Spielberger, 1983) and the BIS/BAS scales (Carver and White, 1994) before the scanning session. While the STAI provides an assessment of anxiety (State-Trait Anxiety Inventory), the BIS/BAS scales assess dispositional sensitivities related respectively to the Behavioral Inhibition System (aversive motivational system) and to the Behavioral Approach System (appetitive motivational system), as proposed by Gray (see Carver and White, 1994; Gray, 1982).

Stimuli

The auditory stimuli were produced by actors and taken from a database previously acquired and analyzed by Banse and Scherer (1996). We used three different tokens of nonsense syllable sequences (pseudo-words: "goster", "niuvenci", and "figotleich") extracted from meaningless sentence-like utterances. These voices were previously judged to express anger or neutral prosody, as validated in earlier behavioral work (Banse and Scherer, 1996), showing an average accuracy of anger recognition of 75%. Male and female speakers were equally counterbalanced across conditions. All the stimuli were matched in term of duration (750 ms). The mean acoustic energy was also matched across stimuli in order to avoid loudness effects.

Experimental design

In order to manipulate voluntary attention orthogonally to emotional prosody, we used a dichotic listening paradigm in which two stimuli were presented simultaneously, one to each ear (anger/neutral [AN], neutral/anger [NA], or neutral/neutral [NN] on the right/left side) on each trial, in pseudorandom order (see Fig. 1). Participants selectively attended to either the left or right ear during two successive blocks (counterbalanced across participants) and performed a gender-decision on the voice heard on the target side. The same pseudo-words (uttered by different speakers) were presented simultaneously, one in each ear, being either neutral on both sides, or angry on one side but neutral on the other (AN, NA, or NN, in randomized order and equal proportion). In total, three different pseudo-words ("goster", "niuvenci" and "figotleich") were used across all participants but their occurrence was counterbalanced such that only two of them were used for each individual participant, with different pairs used in different participants (the third pseudo-word was used in a different fMRI experiment, reported elsewhere; see Grandjean et al., 2005). A total of 120 trials were presented to each participant.

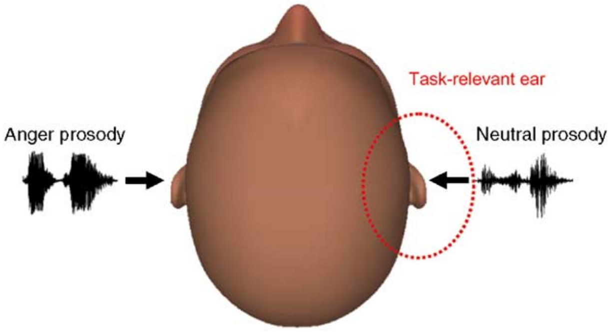

Fig. 1. Experimental paradigm. Participants selectively attended to either the right- or left-sided voice stimulus within a pair, and performed a gender-decision task on the attended stimulus. Orthogonally to the task demands, voices could have a different emotional prosody, either neutral on both sides, angry on the to-be-attended side and neutral on the other side, or vice versa, neutral on the to-be-attended side and angry on the other side.

Imaging and image processing

Functional images were acquired on a 1.5 T Philips system with a GRE EPI sequence (TE/Flip = 40 ms/90°, FOV = 220 mm, matrix = 128 × 128) using BOLD (Blood Oxygenation Level Dependency) contrast. Image volumes consisted of 32 contiguous 3.4 mm axial slices parallel to the inferior occipito-temporal plane, and were acquired using a sparse imaging procedure with a repetition time (TR) of 5 s, including an effective acquisition time (TA) of 2.5 s interleaved with a silent gap of 2.5 s. Auditory stimuli (750 ms duration) were delivered binaurally via MRI-compatible headphones, and were always presented with a varying jitter during the silent gap between each EPI volume (24 different events for each experimental conditions, plus 48 null events without auditory stimulation as a baseline condition). Functional scans were realigned, corrected for slice timing, normalized to the Montreal Neurological Institute (MNI) template (resampled voxel size: 3 × 3 × 3 mm^3), and spatially smoothed (8 mm isotropic FWHM Gaussian kernel) using standard procedures in SPM2 (www.fil.ion.ucl.ac.uk).

Statistical analysis of images

Statistical analysis was performed with SPM2 software (www.fil.ion.ucl.ac.uk). Each event type was modeled as a separate regressor convolved with a canonical hemodynamic response function, and movement parameters from realignment corrections were entered as additional covariates of no interest to account for residual movement artifacts after realignment. Statistical parametric maps were generated from linear contrasts between conditions in each participant. A second-stage random-effect analysis (RFX) was then performed using one-sample t tests on contrast images obtained in each subject for each comparison of interest (df = 13). All analyses were performed across the whole brain (including analyses performed for relevant and irrelevant ear separately). Additional standard ANOVAs were performed on parameter estimates of activity extracted from SPM clusters using Statistica 6.0.

Finally, we tested for any correlation between the brain responses to emotional prosody and anxiety measures from the

STAI and BIS/BAS questionnaires, by performing a whole-brain regression analysis on contrast images of interest (e.g., to-be-attended vs. to-be-ignored anger prosody) using the questionnaire scores from each individual participants, entered as independent linear parametric covariates in a new second-level SPM design matrix. All coordinates (x, y, z) are reported in the MNI space.

Results

Behavioral analysis

Accuracy and reaction times (RTs) were measured during fMRI scanning for each trial and each participant (except for 3 out of 15 participants, whose data were not saved due to technical problems). These behavioral results showed that participants performed the gender judgment task with a high level of accuracy (mean correct = 87.6%). Percentages of correct responses did not significantly differ across all experimental conditions ($\chi^2 = 2.12$, $P > 0.3$). A repeated-measure ANOVA was performed on the mean RTs for correct responses with Attention (right or left ear) and Stimulus Type (NN, AN, NA) as factors after removing outlier values (RTs inferior to 150 ms or superior to twice the mean of a particular condition; 0.5% of the total number of trials). This analysis revealed an interaction between Attention and Stimulus type ($F(2, 22) = 3.3$, $P = 0.056$), but no significant main effect ($F < 1$ in both cases). Subsequent analyses also examined specific contrasts testing for (1) whether anger prosody was “implicitly” processed even though this was not relevant to gender-decision task, (2) whether anger processing showed any asymmetry between the left and right ears/hemispheres, and (3) whether such emotional evaluation could still occur even when angry voices were to-be-ignored. These analyses revealed significantly slower responses when an angry voice was presented in the *left* ear but only when this side was to-be-attended (mean = 1643 ms), relative to the same stimulus condition but with the left ear to-be-ignored (mean = 1558 ms; $F(1,11) = 4.5$, $P = 0.057$), and relative to neutral voices on both sides (mean = 1561 ms; $F(1,11) = 5$, $P < 0.05$). Noteworthy, none of these contrasts was significant when an angry voice was presented in the *right* ear. Other pairwise comparisons between conditions were not significant. Taken together, these behavioral data suggest (1) an effect of anger prosody in the left to-be-attended ear even though emotion was irrelevant to the task, and (2) a superiority of the left-ear/right-hemisphere in processing auditory emotional stimuli (see Borod and Madigan, 2000; Jäncke et al., 2001), here selective to the condition in which anger prosody was to-be-attended. However, there was no behavioral effect of angry prosody when voices were to-be-ignored. Importantly, these data also demonstrate that participants could make equally accurate gender judgments on both angry and neutral voices.

fMRI data analysis

Given that the primary purpose of the current study was to determine how brain responses to emotional prosody are modulated by endogenously-driven spatial attention, we first aimed at distinguishing between (i) brain regions that responded to emotional events independently of the current side of auditory attention, and (ii) brain regions that differentially responded to the same emotional events as a function of auditory spatial attention.

Attention-independent emotional response in middle superior temporal sulcus and amygdala

To identify brain regions responding to emotional prosody irrespective of the target side of auditory attention, we compared activity elicited by stimulus pairs containing an angry voice (AN + NA) relative to pairs containing only neutral voices (NN).

Results revealed strong increases in the middle part of the right superior temporal sulcus (STS) ($x, y, z = 62, -30, 6$; $t = 5.80$; $P < 0.001$ uncorrected; see Fig. 2a), as well as in homologous areas of the left STS ($x, y, z = -60, -24, 0$; $t = 4.43$; $P < 0.001$ uncorrected). These activations were observed irrespective of which ear was the target of attention, indicating that emotional prosody could enhance neural responses in STS even when presented in the task-irrelevant ear (anger vs. neutral in relevant ear: $t > 4.14$; anger vs. neutral in irrelevant ear: $t > 4.35$; $P < 0.001$ uncorrected, for bilateral STS). Even with a low threshold ($P < 0.05$ uncorrected), no interaction between emotion and attention was found in the auditory cortex. Moreover, activations by angry voices in to-be-attended channel and angry voices in the to-be-ignored channel were found to overlap (using combined inclusive masks at $P < 0.005$) and selectively involved STS in both the right ($x, y, z = 60-30$ 3) and left hemisphere ($x, y, z = -60, -27, 3$). The lack of attention effect on STS responses to prosody did not simply reflect insufficient attention to the task-relevant ear, since concomitant effects of attention were observed in several brain regions. Such effects of attention included a general increase in right STS when participants were requested to judge voices from the left rather than the right ear, across all stimulus pairs (main effect of attention; left-side > right-side; $x, y, z = 60, -12, -9$; $t = 3.45$, $P = 0.002$; see Grandjean et al., 2005), as well as increases in orbitofrontal cortex (OFC) and occipital visual areas (see below). More detailed analyses of the pattern of responses in STS regions to voices and acoustically-matched stimuli are reported in Grandjean et al. (2005).

In addition, at slightly lower statistical thresholds, we also found a main effect of anger prosody in the right amygdala ($x, y, z = 27, -6, -15$; $t = 3.15$; $P = 0.004$ uncorrected; see Fig. 2b), where neural responses were increased for stimulus pairs containing an angry voice as compared to pairs of neutral voices, independently of whether the angry voice was to-be-attended or to-be-ignored (anger vs. neutral in relevant ear only: $t = 2.57$, $P = 0.011$; anger vs. neutral in irrelevant ear only: $t = 2.41$, $P = 0.015$). A repeated-measure ANOVA on the parameters of activity extracted from the right amygdala was performed using Attention (right or left ear) and Stimulus Type (NN, AN, NA) as factors. Results confirmed a main effect of Stimulus type ($F(2,28) = 5.5$, $P < 0.01$) but no main effect of Attention ($F < 1$), and no significant interaction effect ($F(2,28) = 1.45$, $P > .25$).

Attention-dependent emotional responses in orbitofrontal and occipital cortex

We then tested for brain areas where activation to emotional relative to neutral prosody would depend on selective attention to the voice, but irrespective of the current side of attention (i.e., right or left ear). We compared activity elicited by anger prosody in the to-be-attended voices (i.e., AN during attention to right ear and NA during attention to left ear), to activity elicited by anger prosody in the to-be-ignored voices (i.e., AN during attention to

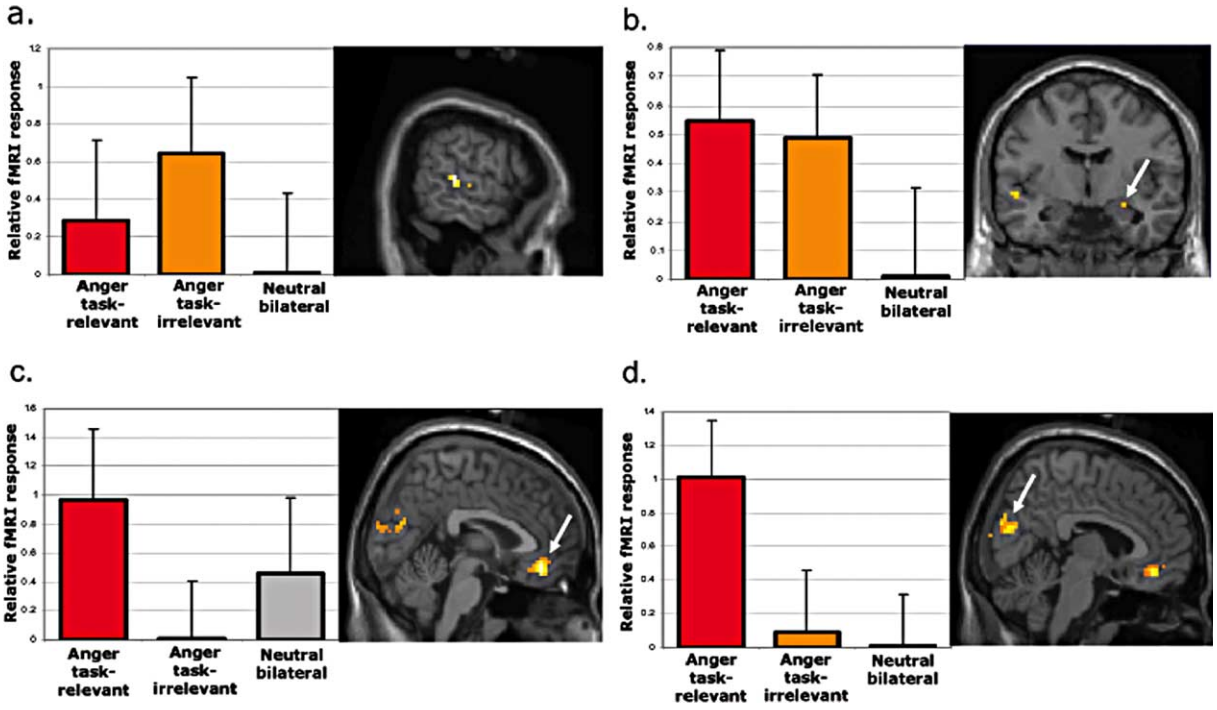

Fig. 2. Brain response to neutral and anger prosody presented to the to-be-attended or to the to-be-ignored ear. Activation maps are superimposed over a sagittal or coronal section of a canonical T1 image. (a) In the right middle superior temporal sulcus (STS), BOLD responses were increased for angry vs. neutral prosody, irrespective of whether anger prosody was presented in the to-be-attended or the to-be-ignored ear (main effect of emotion, $P < 0.001$). Mean parameter estimates of activity (% change relative to the global mean intensity of signal; ± SE) across conditions show an attention-independent emotional response. (b) In the right amygdala (see white arrow), BOLD responses were also increased by pairs containing anger prosody relative to pairs containing only neutral prosody, irrespective of whether anger prosody was presented in the to-be-attended or in the to-be-ignored ear (main effect of emotion, $P < 0.005$). Mean parameter estimates of activity across conditions also show attention-independent emotional responses. (c) In orbitofrontal cortex (OFC, see white arrow), activation was greater to angry voices heard on the to-be-attended side than on the to-be-ignored side (main effect of attention, $P < 0.001$). Mean parameter estimates of activity confirm this attention-dependent emotional response in OFC, but also show that the responses to angry voices on the irrelevant side appeared weaker as compared with neutral voices in both ears. (d) In the cuneus (see white arrow), BOLD responses were increased only when angry voices were on the to-be-attended side, rather than on the to-be-ignored side (main effect of attention, $P < 0.001$). Mean parameter estimates of activity confirm this attention-dependent emotional response.

left ear and NA during attention to right ear), that is, always the same stimulus pairs containing one angry and one neutral voice (AN + NA) but in different task conditions.

When examining this comparison across the whole brain, we found two main regions showing such significant interaction effects between emotion and attention, including the ventromedial part of orbitofrontal cortex (x, y, z = 3, 39, − 12; t = 6.60, $P < 0.001$ uncorrected; $P < 0.05$ corrected at the cluster-level; see Fig. 2c), and the cuneus in medial occipital cortex (x, y, z = 9, − 84, 24; t = 4.72, $P < 0.001$ uncorrected; see Fig. 2d). Furthermore, post hoc tests on the different attention conditions considered separately showed that the cuneus responded significantly more to auditory pairs with angry prosody on the to-be-attended side than to pairs containing neutral prosody only (t = 4.72, $P < 0.001$ uncorrected), whereas no emotional effect was observed when anger was presented on the to-be-ignored side (even with a low threshold, t = 0.11, P = 0.5 uncorrected). However, the pattern of response in OFC was different than that of the cuneus. Post hoc tests performed on the different attention conditions separately showed that although the strong difference between anger on the to-be-attended side and anger on the to-be-ignored side was significant (t = 6.60, $P < 0.001$), OFC tended not only to respond more to angry prosody on the to-be-attended side than to neutral pairs (t = 2.64, P = 0.011) but also tended to respond more to neutral pairs than to pairs with anger on the to-be-ignored side (t = 2.07, P = 0.029) (see Fig. 2c).

In addition, a slightly weaker activation for to-be-attended vs. to-be-ignored angry voices was also found in bilateral ventrolateral prefrontal cortex (right: x, y, z = 57, 27, 6; left: x, y, z = −48, 24, 6), suggesting that this area may also be involved by affective processing under conditions of attention (see Table 1).

By contrast, comparing activations by angry voices on the to-be-attended vs. to-be-ignored side did not reveal any significant differences in bilateral STS and amygdala (see previous section).

Correlation analyses between brain activity and scores at the questionnaires

All our participants had filled in the BIS/BAS scales (Carver and White, 1994) and the STAI-T questionnaire (Spielberger, 1983) before the scanning session. The BIS/BAS scales provide an assessment of dispositional sensitivities related respectively to the behavioral inhibition and approach systems as proposed by Gray (e.g., Gray, 1982), whereas the STAI-T provides an assessment of anxiety traits (Spielberger, 1983). All results described below were obtained by entering the score from each questionnaire and each participant in a further SPM regression analysis using the contrast between anger prosody in the to-be-attended vs. to-be-ignored ear, allowing us to determine whether personality factors assessed by

Table 1
Areas activated in all different contrasts

Brain regions	Brodmann area	Side	Z score	MNI coordinates
Anger vs. Neutral (AN + NA) vs. (NN)				
Superior temporal sulcus	42	Right	4.07	62, −30, 6
Superior temporal sulcus	22	Left	3.45	−60, −24, 0
Posterior parietal	19	Right	3.42	27, −87, 24
Posterior parietal	19	Left	3.71	−33, −72, 36
Inferior frontal gyrus	45	Left	3.61	−54, 24, 21
Superior temporal sulcus	22	Left	3.43	−45, −15, −6
Superior temporal sulcus	22	Right	3.26	60, −15, 0
Anterior cingulate	10	Right	3.25	18, 45, 6
Anger to-be-attended vs. Neutral				
Cuneus	18	Right	4.40	9, −84, 24
Cuneus	19	Right	3.61	27, −90, 21
Superior frontal gyrus	8	Left	3.34	−9, 45, 51
Superior temporal sulcus	22	Left	3.29	−63, −27, 0
Anger to-be-ignored vs. Neutral				
Superior temporal sulcus	22	Right	4.07	66, −30, 3
Superior temporal sulcus	21	Right	3.40	57, −6, −15
Cingulate Gyrus	31	Left	3.56	−3, −45, 30
Inferior frontal gyrus	47	Right	3.36	39, 33, −3
Anger to-be-attended vs. to-be-ignored				
Orbito-frontal gyrus	11	Right	4.38	3, 39, −12
Superior temporal sulcus	39	Right	4.02	33, −57, 27
Claustrum		Left	4.01	−36, 0, 3
Inferior frontal gyrus	47	Left	3.75	−48, 24, 6
Inferior frontal gyrus	47	Right	3.31	57, 27, 6
Cuneus	18	Right	3.59	9, −84, 24
Cuneus	18	Left	3.31	−9, −87, 9
Superior frontal gyrus	10	Left	3.55	−24, 57, 6
Anger to-be-ignored vs. to-be-attended				
Precuneus	7	Right	3.51	9, −54, 39
Parietal lobe	40	Right	3.43	42, −48, 40
Parahippocampal gyrus	30	Left	3.22	−27, −51, 3
Spatial attention towards right vs. left ear				
Parietal lobe	40	Left	3.44	−48, −63, 51
Insula	13	Left	3.27	−36, 21, 6
Spatial attention towards left vs. right ear				
Posterior cingulate	23	Right	4.06	3, −33, 24
Superior temporal sulcus	39	Right	3.99	48, −60, 18
Parietal lobe	40	Right	3.97	60, −39, 48
Parietal lobe	7	Right	3.46	27, −69, 27
Superior temporal sulcus	13	Right	3.17	42, −21, 6
Anterior cingulate	42	Left	3.97	−9, 45, 9
Cuneus	30	Left	3.92	−9, −60, 9
Medial frontal gyrus	9	Right	3.80	6, 54, 18

Areas that were activated for the main contrasts of interest (statistic tests at $P < 0.001$ uncorrected).

STAI and BIS/BAS scales might influence the effect of attention on brain responses to emotional voices. This analysis revealed a significant positive correlation between neural responses evoked by the to-be-attended angry voices in the ventro-medial prefrontal cortex ($x, y, z = 12, 39, -3$) and the BIS dimension of BIS/BAS scales ($r = 0.87$, $P < 0.001$, see Fig. 3), involving a region just slightly above the OFC peak showing an interaction between emotion and attention (see previous section above). There were also positive correlations between the BIS dimension and activations in the right cuneus ($x, y, z = 3, -96, 18$; $r = 0.96$, $P < 0.0001$) and right inferior parietal lobule ($x, y, z = 33, -39, 42$; $r = 0.84$, $P < 0.0005$). On the other hand, regions positively correlating with the BAS dimension were located in the right post-central gyrus ($x, y, z = 63, -21, 30$; $r = 0.89$, $P < 0.0001$) and left inferior parietal lobule ($x, y, z = -36, -45, 57$; $r = 0.85$, $P < 0.0005$).

As can be expected, behavioral scores on the STAI-T were partially correlated with those on the BIS dimension ($r = 0.52$, $P = 0.059$), indicating at least some relation between these two instruments measuring different aspects of anxiety-related traits in personality (the fact that the correlation was only marginally significant may probably reflect the relatively small population). However, our correlation SPM analyses indicated that a different pattern of neural activity was associated with the two measures. Brain regions correlating with the STAI-T were located in the middle frontal gyrus ($x, y, z = -39, 36, 18$; $r = 0.83$, $P < 0.0001$), and in the parahippocampal gyrus ($x, y, z = 30, -45, -15$; $r = 0.94$, $P < 0.0005$), but not found in ventro-medial prefrontal cortex.

Finally, we also entered the score from each questionnaire and each participant in a similar SPM regression analysis using the contrast between anger prosody in the to-be-ignored ear vs. neutral prosody in both ears, allowing us to determine whether anxiety level might influence the effect of emotion on brain responses to angry voices heard outside the current focus of attention (see Bishop et al., 2004; Etkin et al., 2004). However, no significant correlation was found across the whole brain for either STAI or BIS measures (including in the amygdala or the voice-selective STS areas).

Discussion

Using a dichotic-listening paradigm, we show a functional dissociation between brain regions responding to anger prosody independently of current task-relevance (i.e., attended ear side), and brain regions differentially responding to the same emotional cues as a function of such task-relevance. Whereas auditory areas in STS and the amygdala showed a response to angry voices heard either in the to-be-attended or in the to-be-ignored ear, reflecting a relatively obligatory stage in the perception of affective signals, OFC and occipital visual regions responded to angry voices only when these were selectively attended, presumably reflecting more integrative stages of affective evaluation.

Our results show for the first time that amygdala response to anger prosody may dissociate from any concomitant task-related attentional modulation. Although the activation of the amygdala was not very pronounced, this finding clearly parallels previous evidence obtained in the visual domain (e.g., Vuilleumier et al., 2001, 2004) and is relevant to current controversies on the nature and limits of automaticity in affective processing, particularly in relation to amygdala function (Dolan and Vuilleumier, 2003; Ishai et al., 2004; Pessoa and Ungerleider, 2004). Whereas some results indicated that amygdala responses to fearful faces may persist in the presence of reduced cortical responses due to attention (Vuilleumier et al., 2001, 2004), other findings raised the question of whether amygdala activity always require attentive processing (Pessoa et al., 2002). In the current study, the pattern of amygdala activation supports the notion that emotional responses in this

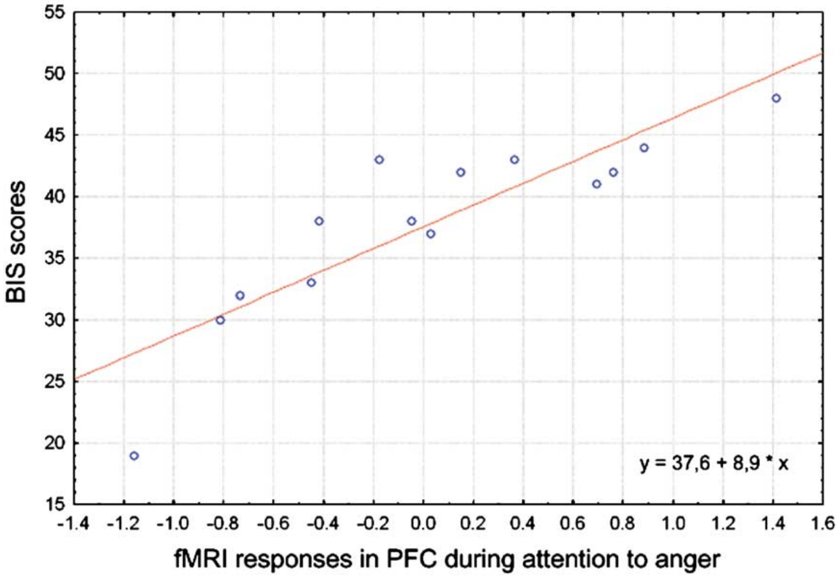

Fig. 3. Scores on the behavioral inhibition system dimension of BIS/BAS scales strongly correlated with the effect of selective attention on emotional response in the ventro-medial prefrontal cortex ($r = 0.87$, $P < 0.001$). The effect of attention on emotional response in the ventro-medial prefrontal cortex was quantified as the difference between the mean parameter estimates of activity (% change relative to the global mean intensity of signal) in this region when anger was presented in relevant ear minus the irrelevant ear.

region may persist independently of endogenously-driven attention, and that this may also exist in the auditory modality, at least under some conditions, despite the concurrent modulation by attention found in other areas of the frontal and occipital lobes. Moreover, this finding is consistent with previous results suggesting that processing of anger in voices was impaired in a patient with amygdala damage (e.g., Scott et al., 1997; but see Anderson and Phelps, 1998).

Furthermore, anger prosody also evoked increased activation in the middle portion of STS as compared with neutral prosody (see also Grandjean et al., 2005). This region corresponds to one of the human brain areas previously reported to exhibit voice-selective responses (Belin et al., 2000), suggesting a category-selective modulation of auditory processing by vocal expression of emotion. These influences of emotion on voice processing in STS provide a striking parallel with similar enhancement found for fusiform cortex in response to faces with fearful expressions (Morris et al., 1998b; Vuilleumier et al., 2001). Our results therefore provide new support to the idea that voice and face perception might share similar principles of brain organization (Belin et al., 2004). Whereas a number of studies have shown that face-selective areas in visual extrastriate cortex are modulated by fearful expressions (Morris et al., 1998b; Vuilleumier et al., 2001), our work show that voice-sensitive areas in auditory cortex may similarly be modulated by the potential threat value of voices (see Grandjean et al., 2005 for details on this specific issue). Moreover, this emotional enhancement in right STS appears distinct from the concurrent modulation of auditory cortical areas by voluntary attention, as we have shown elsewhere (Grandjean et al., 2005). These findings suggest that emotion and attention can both exert separate modulatory influences on auditory processing (Grandjean et al., 2005) and extend previous findings in the visual domain for fearful expressions in faces (Vuilleumier et al., 2001). However, it remains to establish whether such emotional effects in STS are driven by amygdala inputs, for example by testing the effects of amygdala lesion on STS response to emotional prosody as already shown for fusiform responses to fearful faces (Vuilleumier et al., 2004) or by conducting experiments more specifically designed to test for functional connectivity. Alternatively, STS responses to anger might reflect intrinsic computational properties of these brain regions related to social evaluation processes (Winston et al., 2002). In any case, the current brain imaging findings also converge with classic behavioral results during dichotic tasks indicating that the affective meaning of stimuli presented in an ignored auditory channel may nonetheless be still processed to some extent (as for the "own name effect", see Introduction), with such enhancement of auditory cortex response to affectively significant stimuli potentially resulting in some involuntary capture of auditory attention.

In contrast to the attention-independent emotionally-driven enhancement in amygdala and right STS, we found that, for the very same pairs of stimuli containing an angry voice and a neutral voice, the OFC was more activated when the angry voice was to-be-attended than when it was to-be-ignored. This result is consistent with previous findings showing that OFC response to emotional stimuli is enhanced when stimuli, or their emotional value, are attended. For instance, using hybrid stimuli containing faces with different expressions at different spatial frequencies in the image, Winston et al. (2003) demonstrated that emotional information within low-spatial frequencies elicited OFC responses only when this particular frequency band was reported by the participants, suggesting that frontal responses may specifically reflect the conscious emotional percept, whereas increased responses to fearful expressions in the fusiform cortex were independent of conscious percept. Similarly, an event-related fMRI study by Armony and Dolan (2002) also reported bilateral OFC activation when spatial attention was focused on aversively-conditioned faces with angry expressions, relative to a diffuse attention condition. Converging evidence suggests that the OFC is involved in the evaluation of emotionally relevant events across various sensory modalities, including the olfactory (e.g., Anderson et al., 2003; Zald and Pardo, 1997), gustatory (e.g., Small et al., 2003; Kringelbach et al., 2003), touch-related (Rolls et al., 2003), and visual (e.g., Nitschke et al., 2004; Kawasaki et al., 2001) domains. Patients with focal OFC lesions are impaired in personal and social decision-making, and exhibit amodal deficits in the processing of facial and vocal emotional expressions (Damasio, 1994; Hornak et al., 1996, 2003). Previous brain imaging data have also shown that the OFC is involved in the processing of non-vocal auditory emotional events (e.g., Frey et al., 2000), emotional prosody (e.g., Wildgruber et al., 2002, 2004), and in music perception (e.g., Blood and Zatorre, 2000). However, to our knowledge, the current experiment goes beyond these previous works by suggesting that the OFC response to socially relevant auditory stimuli depends on selective endogenously-driven attention.

Based on anatomical and functional data, it has been proposed that the OFC is a convergence region (Mesulam, 1998) that might subserve the integration of multimodal sensory information with affective reactions (Damasio, 1994; Price, 1999; Rolls, 2004). Although the computational mode of processing of OFC is still debated (see Adolphs, 2003; Damasio, 1994; Rolls, 2004; Rule et al., 2002; Wood and Grafman, 2003), there is clear evidence that it plays a critical role in emotional appraisal and social cognition. In particular, it is thought that the OFC is involved in guiding social behavior and social judgments (Adolphs, 2003). Our results may therefore reflect the differential social meaning derived from attended, as compared to unattended, anger prosody in human voices. The OFC might be involved in elaborate aspects of affective appraisal subsequent to the more automatic stages of processing taking place in the amygdala and sensory cortices, integrating this initial evaluation with other cognitive factors related to context, goals, or task demands. Thus, OFC may show different responses to angry voices depending on whether these are currently in the focus of attention and require a behavioral response, and depending on the context provided by other concurrent stimuli present in the environment. Accordingly, the OFC showed a complex pattern of interaction between emotional and attentional factors, not only with the greatest activation when angry voices were heard on the to-be-attended side, but also less response when an angry voice was present in the to-be-ignored ear as compared with neutral voices in both ears (see Fig. 2c). This complex pattern suggests that OFC responses were not only influenced by emotional signals perceived from the to-be-attended voices, but also by emotion implicitly processed on the to-be-ignored side. Although our current hypothesis will need support from future research, an interesting aspect of this pattern of activation is that it might reflect a critical role of OFC in evaluating the *relative* value of concurrent stimuli (e.g., Tremblay and Schultz, 1999) when an action is to be performed on one of them based on the current motivational and task-related goals. Thus, having to ignore an angry voice and select a neutral (or relatively positive as compared to angry) voice might produce a weaker engagement of some appraisal processes and elicit less activity in OFC, as compared to a more ambiguous situation when selecting a neutral voice and ignoring another neutral voice. In other words, whereas the latter condition (attention towards anger) might entail the appraisal of a potentially hostile social signal or conflict, the former condition (attention away from anger) might conversely correspond to an evaluation that threat can be avoided or is not relevant. However, these hypotheses are post hoc and will require further testing, but they seem consistent with the relationships found between emotional responses in these brain regions and proneness to anxiety, as revealed by our correlations with individual personality traits (see below).

We note that we also found an activation in the ventrolateral prefrontal cortex when attention was directed to angry voices, consistent with previous results suggesting an involvement of these regions when people focus on the affective content of visual or auditory stimuli as opposed to when they are merely exposed to such content (Gorno-Tempini et al., 2001; Cunningham et al., 2003; Wildgruber et al., 2005), or when they explicitly categorize socially-relevant faces according to a social rather than perceptual label (Lieberman et al., 2005). These similarities provide support to the hypothesis that affective prosody was evaluated to some extent “implicitly” by our participants, even though their task did not require explicitly to pay attention to emotional aspects of the prosody. Further experiments are needed to investigate the role of these ventrolateral prefrontal areas as a function of the level of processing of self-relevant stimuli.

The correlation analyses between brain responses to emotional prosody and measures from personality scales revealed that the higher our participants scored on the BIS dimension, the greater the effect of selective attention on emotional responses in the ventromedial prefrontal cortex (BA 10) and occipital cuneus (BA 18). This result is particularly interesting given that the BIS has been suggested to reflect individual sensitivity to signals of punishment, with higher scores indicating greater proneness to anxiety when exposed to the proper situational cues (Carver and White, 1994; Gray, 1982). For instance, Carver and White (1994) showed that participants with high BIS sensitivity were more nervous than those with low BIS in a situation where participants anticipated a punishment. In our study, it is plausible that angry voices might convey aversive or negative social signals, possibly of punishment, and that these signals were more extensively processed when they were heard in the to-be-attended ear and required a response, relative to when they could be ignored, leading to a greater engagement of ventro-medial prefrontal cortex as well as visual areas in the attended condition. These results suggest that activity in ventro-medial prefrontal cortex might reflect the tendency to modulate or inhibit behaviors associated with negative outcomes. The correlation in the cuneus might be interpreted either in terms of visual mental imagery or in terms of vigilance: these processes would be enhanced in participants who tend to feel anxious when presented with social signals of punishments (e.g., anger prosody) during attended events. In contrast to what was found by Bishop et al. (2004), in our study, no significant positive relationship was observed between participant’s state of anxiety and amygdala increase of activity to emotional vs. neutral stimuli. However, we found that affective traits measured from BAS and STAI-T scales showed a different pattern of correlation with emotional brain responses (involving parietal regions for the former, as well as middle frontal gyrus and parahippocampal cortex for the latter), possibly reflecting other dimensions of emotional responses that are sensitive to individual differences. A more systematic consideration of anxiety and other personality measures as covariates of interest will certainly constitute a key issue in the future to understand emotion and attention interactions in the processing of self-relevant events.

Moreover, in our study, a striking effect of attention to anger prosody was observed in the visual cortex. The cuneus in medial occipital cortex showed a strong activation by angry voices but only when these were to-be-attended, rather than to-be-ignored. At least two interpretations can be proposed for such visual activation by emotional cues from auditory stimuli. First, activity in this occipital region might reflect a more vivid visual mental imagery (see Kosslyn and Thompson, 2003; Kosslyn et al., 1996) induced by hearing angry voices, specifically when voices were attended. Interestingly, in a study by Platel et al. (1997) investigating the effect of selective attention to different attributes of the same musical stimuli, a greater activity was found in the precuneus/cuneus when participants attended to pitch, rather than to timbre or rhythm, suggesting that different auditory tasks might produce distinct degree of visual mental imagery. In our study, detecting anger prosody in voices from the to-be-attended ear might have induced visual imagery related to the emotional meaning of such voices (e.g., imaging a corresponding face or expression or scene), although we note that such increases arose in a relatively early non-specific extrastriate area rather than in the "fusiform face area". An alternative interpretation accounting for the cuneus activation to anger might involve a multimodal vigilance response elicited by affectively and/or socially relevant events occurring in the focus of attention, leading to a general boosting of sensory cortices beyond the auditory system (see Driver and Spence, 2000). Further research is needed to understand how emotional prosody may affect activity in the visual cortex and interact with selective attention.

In conclusion, our result shows that both the amygdala and the middle STS may respond to emotional cues of anger in voices independently of current task-relevance of the voices, whereas the OFC and cuneus exhibit a differential response to the very same emotional events as a function of selective attention. These results support the proposal that multiple levels of processing are involved in the appraisal of emotional events. Our finding that angry prosody can enhance neural activity in the amygdala and "voice-selective area" in middle STS even when voices are irrelevant to the listener's task (see also Grandjean et al., 2005) indicates that these regions may be involved in a relatively reflexive and automatic stage of emotional appraisal, and provides new support for the notion that sensory cortical processing is differentially influenced by emotion and voluntary attention for both the auditory and visual modalities (Dolan, 2002; Vuilleumier et al., 2004). In addition, our data also provide new evidence that ventral prefrontal regions are involved in processing emotional information conveyed by various sensory modalities, but are modulated by the current behavioral relevance of stimuli and sensitive to individual differences in affective traits. Taken together, our results contribute new cognitive neuroscience evidence for the importance of emotion and attention interactions in social cognition. Future studies might usefully exploit similar approaches manipulating emotional significance and task-relevance of social stimuli to investigate individual differences and psychopathological disorders.

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