

Impact of personality on the cerebral processing of emotional prosody

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ABSTRACT

While several studies have focused on identifying common brain mechanisms governing the decoding of emotional speech melody, interindividual variations in the cerebral processing of prosodic information, in comparison, have received only little attention to date: Albeit, for instance, differences in personality among individuals have been shown to modulate emotional brain responses, personality influences on the neural basis of prosody decoding have not been investigated systematically yet.

Thus, the present study aimed at delineating relationships between interindividual differences in personality and hemodynamic responses evoked by emotional speech melody. To determine personality-dependent modulations of brain reactivity, fMRI activation patterns during the processing of emotional speech cues were acquired from 24 healthy volunteers and subsequently correlated with individual trait measures of extraversion and neuroticism obtained for each participant.

Whereas correlation analysis did not indicate any link between brain activation and extraversion, strong positive correlations between measures of neuroticism and hemodynamic responses of the right amygdala, the left postcentral gyrus as well as medial frontal structures including the right anterior cingulate cortex emerged, suggesting that brain mechanisms mediating the decoding of emotional speech melody may vary depending on differences in neuroticism among individuals. Observed trait-specific modulations are discussed in the light of processing biases as well as differences in emotion control or task strategies which may be associated with the personality trait of neuroticism.

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Introduction

Displays of emotions serve as a valuable behavioral guide in any social situation. Whether it is a smile on the face or tears in the eyes of a person, expressions of emotions not only allow insight into the minds of our communication partners but also regulate social interaction by providing crucial information that helps to adapt one's own behavior to the demands of a given social environment (Van Kleef, 2009).

Besides body gestures, posture and facial signals, human beings rely on speech to infer the emotional messages sent by their communication partners. The words we use allow access to our thoughts and inner feelings. However, often the manner in which we say something appears to “speak louder than words”. Particularly information about a speaker's current affective state might predominantly be conveyed by modulations of speech melody (emotional or affective prosody) rather than word content (Mehrabian and Ferris, 1967; Mehrabian and Wiener, 1967).

Over the past years several studies have addressed the neurobiological mechanisms underlying speech melody perception and have

thereby identified a widespread network of cortical and subcortical structures contributing to the decoding of prosodic information (e.g. reviews in Ackermann et al., 2004; Schirmer and Kotz, 2006; Wildgruber et al., 2006; Wildgruber et al., 2009). Aside the mid and posterior superior temporal cortex, particularly the inferior frontal cortex and orbitofrontal cortex, as well as the basal ganglia and limbic regions have frequently been implicated in the processing of emotional speech melody (e.g. Dara et al., 2008; Ethofer et al., 2006b, 2009; Grandjean et al., 2005; Kotz et al., 2003; Mitchell et al., 2003; Morris et al., 1999; Wiethoff et al., 2008, 2009; Wildgruber et al., 2006; Wildgruber et al., 2002). With respect to hemispheric lateralization, numerous lesion studies indicate a predominant role of the right cerebral hemisphere in the processing of emotional prosody (Borod et al., 2002; Heilman et al., 1984; Ross, 1981; Ross and Monnot, 2008; Starkstein et al., 1994). However, an increasing number of patient data (Adolphs et al., 2002; Cancelliere and Kertesz, 1990; Hornak et al., 2003; Peper and Irle, 1997) as well as neuroimaging data challenge the view of a strict right-ward lateralization of prosody comprehension (Kotz et al., 2006). Considering, for instance, superior temporal structures implicated in prosody processing a recruitment of right (Grandjean et al., 2005; Wildgruber et al., 2005), as well as left (Bach et al., 2008) or both left and right aspects of the superior temporal cortex (Ethofer et al., 2006c, 2009; Mitchell et al., 2003; Wiethoff et al., 2008) has been described in the neuroimaging

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literature. Similarly both an involvement of the right inferior frontal cortex (Buchanan et al., 2000) as well as a bilateral activation of inferior frontal structures (Ethofer et al., 2006b; Ethofer et al., 2009; Wildgruber et al., 2004) have been associated with the processing of prosodic information.

Beyond the mere identification of neural substrates, imaging studies have shed light on the functional properties of several brain regions implicated in prosody processing and in doing so have helped to form hypotheses about the nature of contributions made by these structures to the process of speech melody decoding (review in Wildgruber et al., 2009). For instance: Whereas hemodynamic responses of the mid superior temporal cortex (m-STC) have been characterized to be primarily stimulus-driven (e.g. Ethofer et al., 2009; Wildgruber et al., 2006) and modulated by basic acoustic properties of prosodic stimuli (Wiethoff et al., 2008), activations of the posterior superior temporal cortex (p-STC) as well as inferior frontal areas have frequently been described to be task-dependent and linked to task instructions requiring individuals to focus attention on the classification of vocally expressed emotions (e.g. Ethofer et al., 2006a, 2009; Quadflieg et al., 2008; Wildgruber et al., 2005). Building on such observations, current models of prosody comprehension (Wildgruber et al., 2009) propose hemodynamic activity of the m-STC to reflect processing stages involving acoustic analysis, whereas the p-STC and frontal structures have been implicated in sub-processes concerned with the identification and evaluation of emotions expressed by affective prosody.

However, the ways in which human beings perceive and process their emotional environments tend to differ tremendously across individuals, and the same emotional stimuli may often evoke very different responses among subjects (Hamann and Canli, 2004). Discrepancies in how we perceive and respond to the emotional signals around us most often appear to be determined by differences in personality. A notion which is further supported by personality theories assuming personality styles to modulate an individual's susceptibility to emotional stimulation (Costa and McCrae, 1980; Gray, 1970).

In recent years, functional imaging studies have begun to explore how personality-dependent variations in emotional responsiveness are paralleled by differences in the cerebral processing of emotional cues. Ever since, compelling evidence suggesting a modulating influence of personality on emotional brain responses has steadily accumulated in the literature (Brühl et al., 2011; Canli, 2004; Canli and Amin, 2002; Frühholz et al., 2010; Hamann and Canli, 2004; Hooker et al., 2008).

One of the first reports to relate personality differences to variations in emotional brain reactivity was published by Canli et al. (2001). Using functional magnetic resonance imaging (fMRI), Canli et al. (2001) obtained activation patterns evoked by positive and negative visual emotional stimuli in a sample of fourteen healthy women and correlated those brain responses with individual scores on measures of extraversion and neuroticism, two personality traits which not only have been assumed to influence emotional responsiveness (Costa and McCrae, 1980) but also have been shown to modulate brain activity (e.g. Deckersbach et al., 2006; Fischer et al., 1999; Herrmann et al., 2001; Johnson et al., 1999; O'Gorman et al., 2006). Results indicated a strong association between measures of extraversion and brain responses to positive stimuli within frontal and temporal cortical regions as well as the basal ganglia and amygdala. Furthermore, a significant correlation between measures of neuroticism and hemodynamic activity to negative pictures was observed within the left temporal and left frontal cortex.

However, considering the cerebral basis of prosody decoding, interindividual differences in brain reactivity have largely been overlooked, and modulations of brain activation by basic traits of human personality, to date, have not been investigated systematically. Accordingly, the present study aimed at examining the relationship between measures of personality and hemodynamic response patterns evoked by emotional speech melody. More precisely, we intended to

investigate the influence of personality (particularly the traits of extraversion and neuroticism) on task- and stimulus-driven activity associated with prosody processing. To this end, we presented a set of stimuli comprising digital recordings of words spoken either in a happy, a neutral or an angry tone of voice under three different task conditions: vowel identification, word content identification and prosody identification. During each task, brain activation patterns were obtained using fMRI. Contrasts between task conditions allowed to delineate task-driven activity. Aiming at disentangling activation patterns specific to the identification of affective prosody, we contrasted prosody identification with two further tasks a) vowel identification and b) word content identification, in order to control for (unspecific) hemodynamic responses associated with the processing of a) phonetic or b) semantic aspects of presented speech stimuli. Moreover, contrasts between stimuli spoken in either an emotional or a neutral tone of voice helped to identify stimulus-driven activity. Based on previous neuroimaging studies (e.g. Ethofer et al., 2009; Mitchell et al., 2003; Quadflieg et al., 2008; Wildgruber et al., 2005; Wiethoff et al., 2008), we assumed task-related effects to present as strong hemodynamic responses within the p-STC and frontal cortical regions, whereas stimulus-driven activation was expected within the m-STC. Finally, to investigate personality-dependent modulation of brain responses, activation patterns were correlated with individual measures of personality. We focused our analysis on determining effects of neuroticism and extraversion as those two traits have repeatedly been linked to emotional experience and emotion processing (e.g. Costa and McCrae, 1980; Knyazev et al., 2008; Larsen and Ketelaar, 1991).

While previous studies have targeted the relationships between personality and stimulus-driven emotional brain responses (e.g. Canli et al., 2001; Cremers et al., 2010; Suslow et al., 2010), personality-dependent modulations of task-related activation patterns, in comparisons, have received far less attention. However with respect to reports revealing a strong impact of personality on stimulus-driven emotional brain responses and empirical evidence demonstrating a strong influence of neuroticism and extraversion on brain activation associated with various task conditions unrelated to emotion processing (Haier et al., 1987; Kumari et al., 2004; Stenberg et al., 1993) or even on brain responses at rest (Deckersbach et al., 2006; Fischer et al., 1999; Johnson et al., 1999; O'Gorman et al., 2006), we assumed that both task- and stimulus-driven activation patterns would be modulated by individual differences in personality. Moreover, based on the literature reviewed above, we predicted that such personality-dependent modulation would take place both in cortical, especially frontal and temporal cortical areas as well as subcortical structures, particularly the basal ganglia and amygdalae.

Methods

Participants

Twenty-four volunteers (12 female, 12 male, mean age: 23.3 year, range: 19–33 years) participated in this study. All participants were native speakers of German and right-handed as determined by the Edinburgh Handedness Inventory (Oldfield, 1971). None of the subjects reported any current or past psychiatric or neurological illness, nor indicated any hearing impairments.

Prior to their enrolment in this study all volunteers received detailed information about purpose and procedure of the investigation as well as a thorough screening concerning standard MRI contraindications. Participation was based upon written consent.

Ethics statement

The present study was conducted in accordance with the ethical principals expressed in the Declaration of Helsinki, and the study protocol was approved by the local ethics committee.

Tasks and stimulus material

During scanning, all participants were instructed to complete three tasks: 1) identification of vowels 2) identification of emotional prosody 3) identification of emotional semantics (i.e. word content). During vowel identification (VI), each individual was asked to indicate whether a spoken word contained the letter “a”, or the letter “o”, or whether neither “a”, nor “o” were present. Prosody identification (PI) required participants to label emotions conveyed by the speakers’ tone of voice choosing one of three alternatives: happy, neutral or angry. Similarly, the semantics identification (SI) task asked to classify each stimulus according to its emotional word content using one of three categories: positive, neutral or negative word meaning. Each task was presented twice, with the same set of stimuli used throughout all tasks. Stimulus order within tasks was fully randomized and task order was balanced among individuals and repetitions.

Stimulus material comprised short digital recordings of sixty single German words (30 adjectives, 30 nouns) spoken by six professional actors (three female, three male) either in a happy, an angry or a neutral tone of voice. Stimulus material was balanced with respect to prosodic category (20 words spoken in a happy, 20 in a neutral and 20 in an angry tone of voice), word content (20 words with positive, 20 with neutral, and 20 with negative meaning; a-priori categorization based on previous ratings obtained by [Herbert and collaborators \(2006\)](#)) and occurrence of vowels (20 words containing the vowel “a”, 20 words containing the vowel “o”, 20 word with neither “a” nor “o”). To ensure that emotional prosody was manipulated as intended, stimulus material was pretested in two pilot studies (pilot study 1: 20 subjects, 10 male, 10 female; pilot study 2: 10 subjects, 5 male, 5 female) and stimuli were only considered for use in this main experiment if they were correctly classified by at least 70% of the participants involved in both pilot studies.

All auditory stimuli were normalized to the same mean intensity and presented binaurally via MR compatible headphones (MRIconfon; Innomed, Magdeburg, Germany). Stimulus duration ranged from 480 ms to 1440 ms, with a mean duration of 994 ms (standard deviation: ± 244 ms) obtained for stimuli spoken in an angry tone of voice; 853 ms (± 146 ms) for stimuli spoken in a happy tone of voice and 760 ms (± 230 ms) for stimuli spoken in a neutral tone of voice.

During each task, participants indicated their answers by pressing one of three buttons on a fiber optic response system (LumiTouch, Photon Control, Burnaby, Canada) with their right hand. Responses were required within a time frame of three seconds following stimulus onset. Handling of response equipment was explained immediately before starting each task and visual aid concerning response categories was provided throughout the whole scanning session. To avoid effects attributable to the positioning of categories on the response pad, arrangement of response categories was reversed for half of the participants.

Personality measures

To evaluate personality, a German version ([Borkenau and Ostendorf, 2008](#)) of the NEO-Five Factor Inventory (NEO-FFI; [Costa and McCrae, 1991](#)) was employed. The NEO-FFI is a widely accepted self-report questionnaire that allows to assess five central traits of adult personality: neuroticism, extraversion, openness, conscientiousness, agreeableness. Measures for each personality dimension are obtained using 60 statements (12 items per trait subscale) paraphrasing cognition and behavior typical of the traits of interest. Participants are required to indicate the extent of their agreement with each statement using a 5-point rating scale ranging from strongly disagree to strongly agree. To determine individual scores for each personality dimension, ratings are averaged among items within each subscale resulting in scores ranging from 0 to 4 per trait with higher scores indicating higher degrees of trait manifestation. Of those traits

assessed by the questionnaire, only measures of neuroticism and extraversion were regarded in this study.

Within our sample, trait scores obtained for extraversion ranged from 1.08 to 3.42 with a mean total score of 2.39 ± 0.52 determined for this personality dimension. Neuroticism scores ranged from 0.25 to 2.67 averaging to a mean total score of 1.69 ± 0.62 .

Magnetic resonance imaging: Data acquisition

MR images were acquired using a 3T whole body scanner (Siemens VERIO, Siemens Erlangen, Germany) equipped with a standard 32 channel head coil. Functional images were obtained with a 2-dimensional echo-planar imaging sequence covering the whole brain (EPI: TR = 2000 ms, TE = 30 ms, flip angle = 90° , field of view (FOV) = 192 mm, 64×64 matrix, 34 slices, 3 mm thickness, 1 mm gap, oriented along AC-PC plane). Functional image acquisition and stimulus presentation were synchronized. Stimulus onset was jittered relative to scan onset in steps of 500 ms and inter-stimulus-intervals ranged from 7 to 9 s. Null-events were randomly interspersed throughout stimulus presentation (10% null events within one run). Functional images for each task and task repetition were obtained within separate runs with 279 volumes acquired per run. Thus, the experiment incorporated six functional runs (three tasks repeated twice) adding up to a total scan time of approximately 60 min. Additionally, high-resolution structural images were acquired using a magnetization prepared rapid acquisition gradient echo (MPRAGE) sequence (TR = 1900 ms, TE = 2.52 ms, 176 slices with 1 mm thickness). Finally, to allow offline correction of EPI distortion a static field map (TR = 488 ms, TE(1) = 4.92 ms, TE(2) = 7.38 ms) was obtained for each subject prior to functional measurements.

Data analysis

Behavioral data

To assure constant attention to and correct understanding of task requirements, the performance of each participant was monitored and logged during scanning. For each subject, mean reaction times as well as mean accuracy rates (= number of stimuli correctly identified divided by the number of stimuli presented multiplied with 100) computed for each task and prosodic category were regarded as measures of general performance. In order to infer differences in performance among tasks and prosodic categories, obtained mean accuracy rates and reaction times were subjected to two separate repeated-measures analyses of variance (ANOVA) with task (VI, PI, SI) and prosodic category (happy/neutral/angry) defined as within-subject factors. To account for violations of sphericity, p-values were Greenhouse–Geisser corrected.

Moreover, to investigate possible relationships between personality and performance, correlations between trait scores (extraversion, neuroticism) and individual performance measures (accuracy rates, reaction times) were assessed using Pearson's coefficient.

MRI data

Imaging data was analyzed using SPM5 software (Wellcome Department of Imaging Neuroscience, London, UK; <http://www.fil.ion.ucl.ac.uk/spm>). To exclude measurements preceding T₁ equilibrium, the first five EPI images obtained within each run were discarded from further analysis. All images were realigned to the first volume, unwarped using a static field maps ([Andersson et al., 2001](#)), corrected for slice timing, coregistered with anatomical images, normalized to MNI space ([Collins et al., 1994](#)) and finally smoothed using a isotropic Gaussian kernel of 10 mm full-width half-maximum. Statistical analysis was based on a general linear model ([Friston et al., 1994](#)) with a separate regressor defined for each event using a stick function convolved with the hemodynamic response function. Events were time-locked to stimulus onset. Low frequency components were

removed from the data by applying a high-pass filter with a cut-off frequency of 1/128 Hz. To account for serial autocorrelation within the data, the error term was modelled as an autoregressive process (Friston et al., 2002).

For each subject, individual activation maps reflecting task- and stimulus-driven effects were calculated using t-contrasts of parameter estimates (β -weights): To examine task-specific effects, activation during prosody identification was compared to activation observed during both word content identification and vowel identification [PI > (SI, VI)]. Moreover, to evaluate stimulus-driven effects, hemodynamic activity to emotionally spoken stimuli was contrasted to cerebral responses obtained for neutrally spoken ones [(happy,angry) > neutral]. In order to further delineate stimulus-driven effects, additionally comparisons between happy and angry prosody were computed (happy > angry; angry > happy).

Statistical evaluation of group data was based on a second level random-effects analysis. Results are reported at a height threshold $p \leq 0.001$ ($T \geq 3.48$), corrected for multiple comparisons across the whole brain at cluster level ($p \leq 0.05$). For activations within predefined region of interest (ROI), the search volume was restricted to these regions, and corrections for multiple comparisons were performed using a small volume correction (Worsley et al., 1996). As described in the Introduction, we expected stimulus-driven activation within the left and right m-STC, whereas task-specific responses were expected within the right p-STC and right IFC. Thus ROIs comprised the right and left superior temporal gyrus as well as the inferior frontal cortex (pars opercularis, pars triangularis, pars orbitalis of the inferior frontal gyrus). Each ROI was defined using the automatic anatomic labeling (Tzourio-Mazoyer et al., 2002) tool implemented in the WFU pickatlas (Maldjian et al., 2003). Moreover, to assure that observed stimulus-driven effects were not solely attributable to slight discrepancies in stimulus duration among prosodic categories, mean parameter estimates for each stimulus event were extracted from each cluster showing significant stimulus-driven activation. Subsequently mean parameter estimates obtained for each participant were subjected to simple regression analyses with stimulus durations defined as independent variable and mean parameter estimates for each corresponding stimulus event as dependent variable. Regression residuals were averaged among prosodic categories (happy, angry, neutral) and compared among categories using paired-sample t-test ((happy,angry) vs. neutral, happy vs. angry) to assess whether obtained stimulus-driven effects remained significant after controlling for differences in stimulus duration.

Finally, to evaluate brain activity varying with personality, correlations between brain activity and trait scores of neuroticism and extraversion were determined using regression analyses on contrast

images with trait scores entered as covariates into the regression model. Correlations were assessed separately for each trait. Results are reported at a height threshold of $p \leq 0.001$ ($T \geq 3.48$), corrected for multiple comparisons across the whole brain at cluster level ($p \leq 0.05$). Again, for activation within predefined ROIs, search volume was restricted to these regions and corrections for multiple comparisons were performed using a small volume correction (Worsley et al., 1996). ROIs comprised the basal ganglia (putamen, pallidus, caudate), amygdala, frontal cortex (superior, mid and inferior frontal gyrus) and temporal cortex (superior, mid and inferior temporal gyrus) of both hemispheres.

Results

Behavioral data

Accuracy rates (Fig. 1A)

Data analysis revealed a significant main effect of task [$F(1.66, 38.11) = 12.81, p = 0.000$] as well as a significant interaction of task and prosodic category [$F(3.17, 72.95) = 4.14, p = 0.008$], whereas the main effect of prosodic category failed to reach statistical significance [$F(1.62, 37.16) = 3.33, p = 0.056$]. To further delineate observed task effects, mean accuracy scores were compared among tasks using paired samples t-tests. Results revealed significant accuracy differences between VI and PI ($t(23) = -5.03, p = 0.000$) as well as between VI and SI ($t(23) = -4.69, p = 0.000$) with higher proportions of correct responses obtained for VI (mean \pm standard deviation: $96\% \pm 4\%$) as compared to both PI ($88\% \pm 9\%$) and SI ($88\% \pm 8\%$). Moreover, in order to explore the task \times prosodic category interaction, differences among prosodic categories were analyzed separately for each task using repeated-measures ANOVAs with prosodic category (happy/neutral/angry) treated as within-subject factor. Pair-wise comparisons among prosodic categories within each task helped to detail the finding. A significant effect of prosodic category was revealed only for PI [$F(1.68, 38.66) = 4.96, p = 0.016$] with higher accuracy in judging neutral ($91\% \pm 10\%$; $t(23) = -2.53, p = 0.016$) and angry ($89\% \pm 10\%$; $t(23) = -2.214, p = 0.037$) prosody as compared to happy ($84\% \pm 13\%$) prosody. During SI and VI, however, all stimuli, regardless of whether they were spoken with an angry, a happy or a neutral tone of voice, were judged with similar precision (Fig. 1A).

Reactions times (Fig. 1B)

Concerning reaction times, no significant main effect of task [$F(1.60, 36.50) = 1.71, p = 0.198$] or interaction of task and prosodic category [$F(2.81, 64.85) = 0.62, p = 0.597$] was revealed. However,

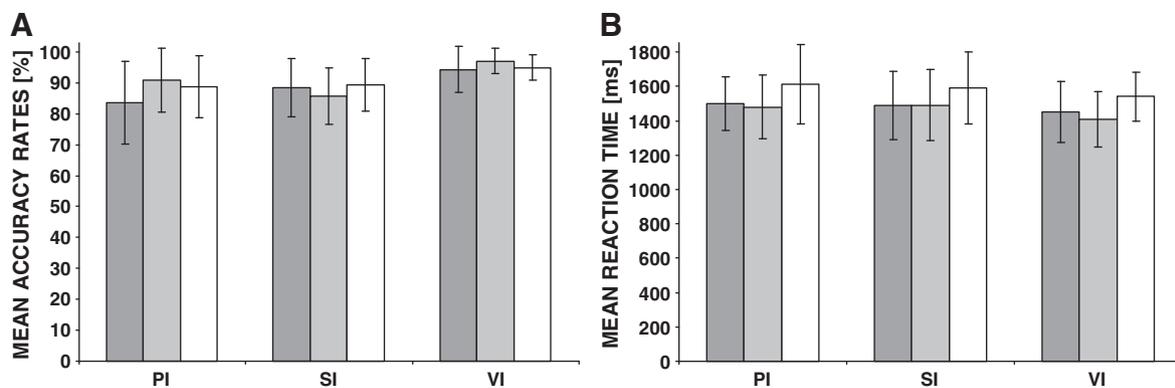


Fig. 1. Behavioural data: Mean accuracy rates (left panel) and mean responses times (right panel) obtained within each task (VI = vowel identification, PI = prosody identification, SI = semantics identification) for stimuli spoken in either a happy (dark grey bars), neutral (light grey bars) or angry tone (white bars) of voice. Error bars indicate standard deviations from the mean.

Table 1

Task-specific activation: significant results obtained from contrasting prosody identification (PI) against both vowel identification (VI) and word content identification (SI).

Contrast	Anatomical definition	Cluster size	T	p (corr.)	Cluster peak		
					x	y	z
PI>(SI, VI)	R: IFC	586	6.31	0.000	54	33	18
	R: p-STC	18	4.39	0.035	60	-48	15 *

Height threshold $T \geq 3.48$, $p \leq 0.05$ corrected for multiple comparisons at cluster-level across the whole brain, *corrected for multiple comparisons within the respective ROI; R: right cerebral hemisphere / L: left cerebral hemisphere; IFC: inferior frontal cortex / p-STC: posterior superior temporal cortex.

data analysis did indicate a significant main effect of prosodic category [$F(1.94, 44.63) = 47.83$, $p = 0.000$]. Paired samples t -test among prosodic categories revealed significant response time differences for comparisons computed between happy and angry ($t(23) = -8.33$, $p = 0.001$) as well as between neutral and angry ($t(23) = -8.60$, $p = 0.000$). Corresponding mean response times indicated slower responses following angrily (mean \pm standard deviation: $1582 \text{ ms} \pm 157 \text{ ms}$) as compared to happily ($1480 \text{ ms} \pm 146 \text{ ms}$) or neutrally ($1461 \text{ ms} \pm 138 \text{ ms}$) spoken stimuli. To control for effects attributable to differences in stimulus durations, the computed analyses were repeated using measures of reaction time from which all variance correlated with stimulus duration had been removed. To this end, reaction times obtained for each stimulus were entered into a simple regression analysis with stimulus duration modelled as regressor and the resulting regression residuals were subsequently subjected to an analysis of variance with task and prosodic category defined as within-subject factor, as well as post-hoc t -test to further evaluate the findings. Results indicated that, irrespective of task condition, 49% of the variance in response times was explained by differences in stimulus durations ($R^2 = .485$, $p = 0.000$). However, the reported main effect of prosodic category remained significant [$F(1.95, 44.93) = 3.67$, $p = 0.034$] even after controlling for differences in stimulus duration, with statistics computed on regression residual indicating a significant response time difference between angry and happy prosody ($t(23) = -2.54$, $p = 0.018$) (Fig. 1B).

Relationship between trait scores and performance measures

Correlation analyses revealed significant associations between trait scores for extraversion and accuracy rates obtained during SI ($r = 0.63$, $p = 0.001$) as well as between extraversion and accuracy scores computed for the judgment of neutrally ($r = 0.51$, $p = 0.012$) and angrily ($r = 0.46$, $p = 0.022$) spoken stimulus material. However, no further significant correlations did emerge between measures of performance and personality variables.

Imaging data

Task-related activity (Fig. 2)

To evaluate activation patterns specific to prosody judgment, hemodynamic responses obtained during PI were compared to responses obtained both during SI and VI [PI>(SI, VI)]. Results are summarized in Table 1. Data analysis yielded enhanced activation of the right inferior frontal cortex as well as the right posterior superior temporal cortex during prosody judgement as compared to word content and vowel identification (Fig. 2).

Stimulus-driven activity (Fig. 3)

To determine stimulus-driven effects, activation patterns to words spoken with emotional (i.e. happy and angry) prosody were compared to brain activity evoked by neutrally spoken stimulus material [(happy, angry)>neutral]. Results are displayed in Table 2. Stronger responses to emotional as compared to neutral prosody were observed within the left and right superior temporal gyrus, the left pre- and postcentral cortex as well as the medial frontal cortex. Aiming to further delineate stimulus-driven effects, comparisons between happy and angry stimulus material were computed. Relative to angry stimuli, enhanced activation of the right anterior cingulate cortex was observed during the perception of happily spoken stimuli. Vice versa, relative to happy stimuli, the presentation of angry prosody was associated with increased responses of the left and right superior temporal gyrus. Reported stimulus-driven effects on brain activation could not be explained by discrepancies in stimulus duration among compared prosodic categories, as described activation differences (i.e. differences in parameter estimates) remained significant after controlling for effects of stimulus duration by means of regression analyses and statistics computed on resulting residuals (please refer to Table 2, column *residual statistics* for details on results) (Fig. 3).

Correlations between brain activity and measures of personality (Fig. 4)

To investigate personality-dependent modulation of task- and stimulus-driven activation patterns, brain responses obtained for each contrast were correlated with individual measures of personality. The employed correlation analysis failed to reveal a significant association between brain activity and measures of extraversion. However, the analysis did indicate a significant positive correlation between trait scores for neuroticism and neuronal responses within the right amygdala, the right medial frontal cortex including aspects of the anterior cingulate cortex as well as the left postcentral cortex during prosody judgment as relative to word content and vowel evaluation (Table 3). Moreover, a positive correlation between neuroticism scores and cerebral activity to happy prosody as compared to angry prosody was observed within the medial frontal cortex (Table 3) (Fig. 4).



Fig. 2. Task-related activation patterns obtained by contrasting brain responses during prosody identification against brain responses during both word content identification and vowel identification (PI>(SI,VI); $p \leq 0.001$ ($T \geq 3.48$), corrected for multiple comparisons at cluster-level). Activation maps are rendered on to the cortical surface of a template brain.

Table 2

Stimulus-driven activation: significant results obtained from contrasts computed among prosodic categories (EMO: happy (HAP), angry (ANG); NEU: neutral).

Contrast	Anatomical definition	Cluster size	T	p (corr.)	Cluster peak			Residuals statistic	
					x	y	z	T	p
EMO>NEU	L: m-STC/ p-STC	577	14.76	0.000	-42	-36	12	5.21	0.000
	R: m-STC	402	14.19	0.000	48	-21	6	3.90	0.001
	R: MFC	351	6.22	0.000	3	54	33	5.42	0.000
HAP>ANG	L: pre-/ postcentral cortex	152	5.92	0.001	-51	-9	45	3.19	0.004
	R: ACC	102	4.73	0.010	6	33	-6	4.31	0.000
ANG>HAP	L: m-STC	455	14.17	0.000	-51	-21	6	3.31	0.003
	R: m-STC/ p-STC	390	11.85	0.000	66	-21	6	3.57	0.002

Height threshold $T \geq 3.48$, $p \leq 0.05$ corrected for multiple comparisons at cluster-level across the whole brain, * corrected for multiple comparisons within the respective ROI; R: right cerebral hemisphere / L: left cerebral hemisphere; m-STC: mid superior temporal cortex, p-STC: posterior superior temporal cortex, MFC: medial frontal cortex, ACC: anterior cingulate cortex.

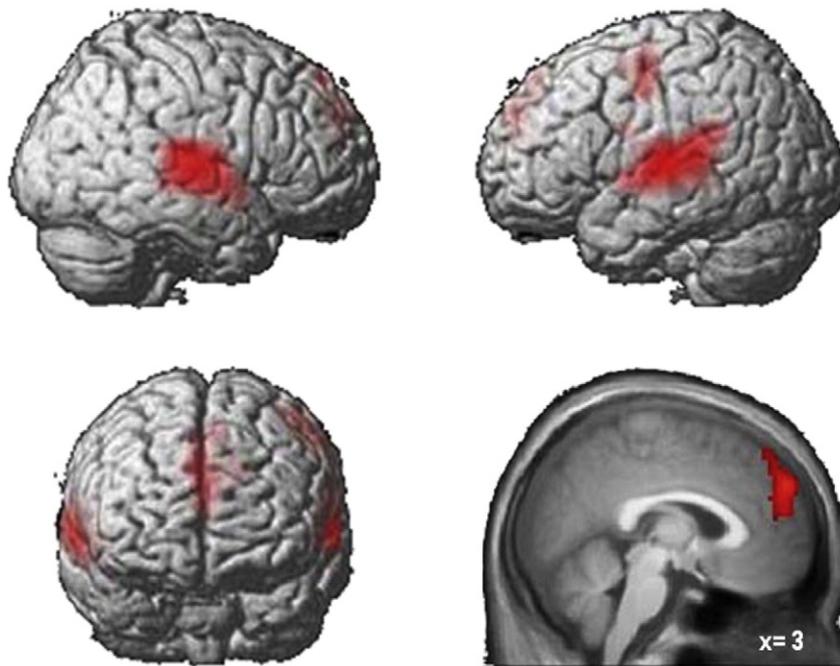


Fig. 3. Stimulus-driven activation patterns obtained by contrasting brain response to emotional prosody against brain responses to neutral prosody ((happy, angry)>neutral; $p \leq 0.001$ ($T \geq 3.48$), corrected for multiple comparisons at cluster-level). Activation maps are rendered on to the cortical surface of a template brain and a sagittal slice obtained at $x = 3$.

Discussion

Summary

Whereas past research has helped to delineate common brain mechanisms subserving the decoding of emotion speech melody, thus

Table 3

Significant correlations between measures of neuroticism and task-related, as well as stimulus-driven brain activation.

Contrast	Anatomical definition	Cluster size	T	p (corr.)	Cluster peak		
					x	y	z
PI>(SI, VI)	R: MFC/ACC	66	5.91	0.034	15	36	12
	L: postcentral cortex	61	5.56	0.045	-45	-36	57
	R: amygdala	8	3.95	0.011	27	3	-21
HAP>ANG	L: MFC	130	6.25	0.002	-18	57	3

Height threshold $T \geq 3.48$, $p \leq 0.05$ corrected for multiple comparisons at cluster-level across the whole brain, * corrected for multiple comparisons within the respective ROI; R: right cerebral hemisphere / L: left cerebral hemisphere; ACC: anterior cingulate cortex, MFC: medial frontal cortex.

far, in contrast, only very little is known about individual differences in the processing of emotional prosody. Accordingly, the present study sought to investigate the influence of individual differences in personality on brain activity related to the decoding of emotional speech melody. To this end, brain responses to emotional prosody were obtained by means of fMRI and subsequently correlated with measures of extraversion and neuroticism, two personality traits which have been suggested to modulate emotional experience and emotion processing (e.g. Costa and McCrae, 1980; Knyazev et al., 2008; Larsen and Ketelaar, 1991).

As far as the influence of extraversion is concerned, the employed data analysis did not reveal any significant correlations between cerebral responses and measures of extraversion. Thus, our findings do not provide evidence for an impact of extraversion on activation patterns associated with the processing of affective prosody. However, strong positive correlation between measures of neuroticism and task-driven as well as stimulus-driven brain activity emerged within several cortical and subcortical structures indicating that the cerebral mechanisms mediating prosody processing might indeed vary depending on individual differences in neuroticism.

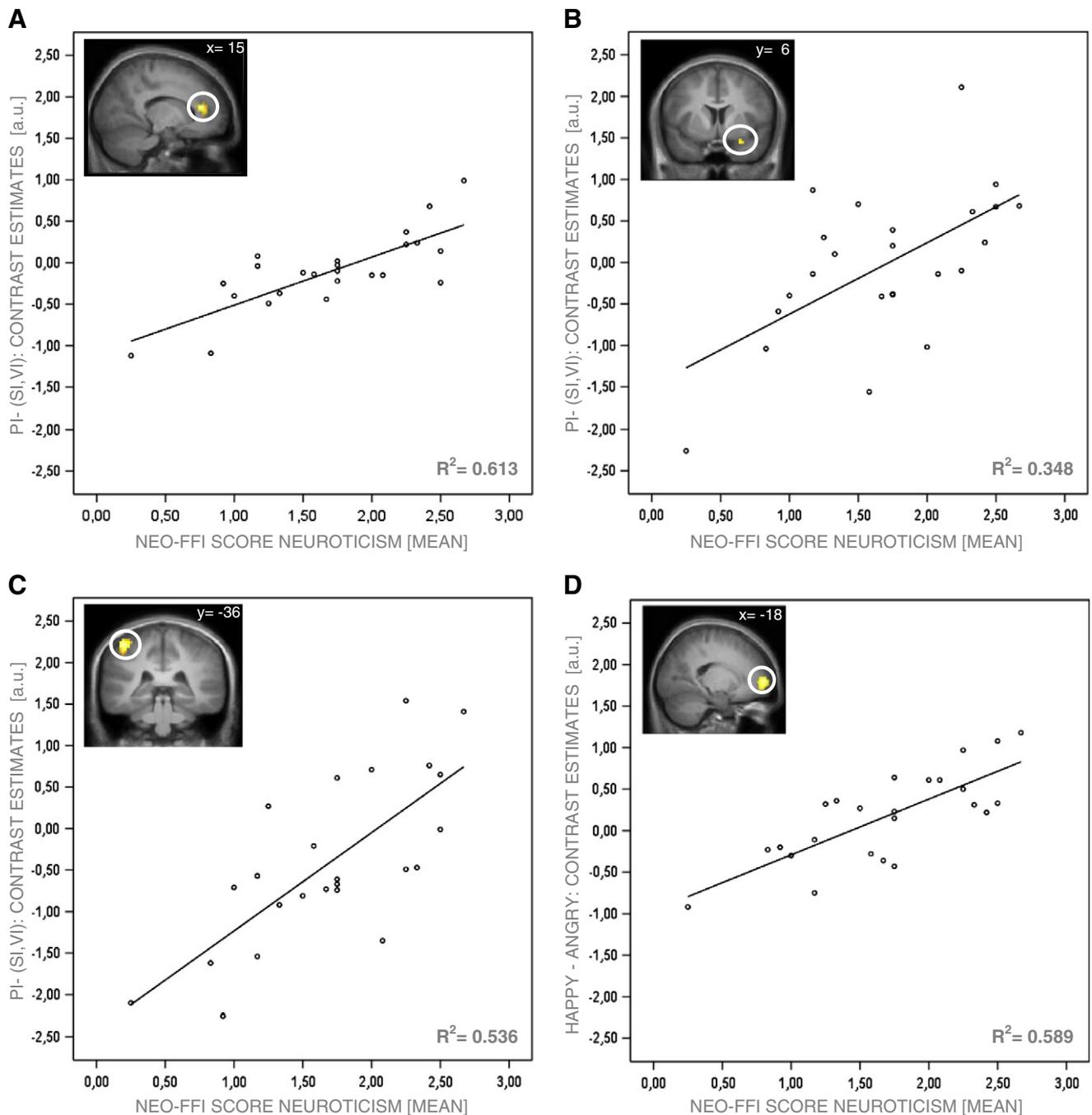


Fig. 4. Scatter plots (and regression lines) depicting relationships between measures of neuroticism (x-axis: mean NEO-FFI score) and brain responses (y-axis: contrast estimates) presented for clusters in which a significant correlation between neuroticism and task-related (panels A–C: A—the right medial frontal cortex including aspects of the anterior cingulate cortex; B—the right amygdala, C—the left postcentral gyrus) as well as stimulus-driven brain reactivity (panel D—anterior rostral medial frontal cortex) emerged. Contrast estimates were extracted from each voxel within displayed clusters (please see inserts in the left upper corner of each panel) and subsequently averaged among voxels within the respective cluster.

Task-related activity and its modulation by personality traits

In accordance with previous findings (e.g. Ethofer et al., 2009; Mitchell et al., 2003; Quadflieg et al., 2008; Wildgruber et al., 2005), task-related differences in brain activation were observed within the right inferior frontal cortex (IFC) as well as the right posterior superior temporal cortex (p-STC): Hemodynamic responses within the IFC and p-STC showed to be more pronounced when subjects' attention was focused on the decoding of affective prosody as compared to when attention was directed to the identification of

phonetic or semantic aspects of a given speech stimulus which corroborates past suggestions of a key contribution of both structures to processing steps concerned with the explicit evaluation of emotional information express by speech prosody (Wildgruber et al., 2006, 2009).

However, task-related activation patterns, further, appeared to be modulated by interindividual differences in personality. As evidenced by a strong association between trait measures of neuroticism and hemodynamic activity within left postcentral as well as limbic areas (right anterior cingulate cortex and right amygdale), particularly

differences in neuroticisms appeared to exert great influence on brain responses associated with speech prosody judgment.

Although limbic regions have frequently been recognized as key structures of the “emotional brain” (Dalglish, 2004), their role in the decoding of emotional speech melody remains controversial: For instance, considering the contribution of the amygdala, previous studies suggest increased (Wiethoff et al., 2009) as well as decreased (Morris et al., 1999) or no “critical” (Adolphs and Tranel, 1999) amygdalar involvement during the processing of vocally expressed emotions. Such inconsistencies in the literature have partly been resolved by applying a dual-process concept to prosody comprehension positing explicit and implicit processing mechanisms each of which in turn are assumed to be differentially represented in the brain (Wildgruber et al., 2006, 2009). Observed involvement of limbic structures, thus, might depend upon whether employed tasks address cognitive-controlled (explicit) or rather incidental (implicit) modes of prosody processing. As far as the neural substrates of both types of processing are concerned, experimental data highlight a predominant role of limbic structures during implicit processing, whereas explicit processing has been associated with frontal cortical regions (Bach et al., 2008; Hariri et al., 2003; Lange et al., 2003; Sander et al., 2005; Tamietto and de Gelder, 2010; Wildgruber et al., 2006, 2009). Moreover, recent neuroimaging studies have suggested that frontal cortical areas might also contribute to the inhibition of limbic activation when individuals actively attend to emotional signals (Blair et al., 2007; Mitchell et al., 2007). Considering the functional role of those observations, suppression of limbic activity might reflect a recruitment of emotion regulation processes during task performance (Blair et al., 2007) which in turn might attenuate the automatic induction of specific emotional reactions associated with limbic activation during implicit prosody processing (Wildgruber et al., 2009). In keeping with the idea that emotional responses may impair our ability to perform goal-directed task (Blair et al., 2007), the value of described adaptations of limbic activation thus appears to lie in aiding task performance.

However, in light of a strong association between neuroticism and limbic brain responses under explicit processing conditions (as required by the PI task), proposed emotional regulation processes and thus the suppression of predominant emotional responses appears to be altered in individuals reporting higher degrees of neuroticism. Various features associated with “neurotic” personality profiles lend themselves to the assumption of altered emotional regulation. For example, affective instability, a “trademark” of the neuroticism concept incorporated in the NEO-FFI (Borkenau and Ostendorf, 2008) might itself reflect a failure to modulate emotional responses appropriately. Altered emotional regulations might in turn render “neurotic” subjects more sensitive to emotional (particularly aversive) stimulation as documented for instance by a variety of psychophysiological studies conducted in clinical (e.g. Lewinsohn et al., 1973; Marissen et al., 2010; Sigmon and Nelson-Gray, 1992) as well as nonclinical samples (Norris et al., 2007) scoring high on measures of neuroticism. As for the case of prosody processing, such heightened susceptibility to emotional stimulation associated with alterations in regulatory capacities might be reflected in observed increased limbic activation yielding an automatic induction of emotional responses to presented speech cues.

With reference to the idea that emotional control might aid task performance, one would expect proposed alterations in emotion regulation to be accompanied by deficits in accuracy or speed of task execution. However, behavioral data obtained within this study did not indicate any link between neuroticism and measures of task performance.

Rather than alterations in emotional regulation, observed differences in activation patterns could also reflect discrepant, nonetheless equally efficient approaches taken to tasks requiring the decoding of emotional cues. Bearing in mind that observed limbic activation has

frequently been linked to the induction of emotional responses “neurotic” individuals might rely on feeling rather than thinking when faced with emotional judgments. Similar ideas may be derived considering differences in post-central activation observed in this study.

Aside limbic brain structures, trait-specific modulations of activation were revealed within the left postcentral cortex with enhanced postcentral activity observed in subjects scoring higher in neuroticism. Although primarily recognized for their role in somatosensory processing, left postcentral structures have previously been reported to be involved in emotional task (Canli et al., 2002; Deeley et al., 2006) and activation of somatosensory-related cortices observed during emotion recognition has been associated with simulation processes that aid emotion decoding by generating somatosensory representations that mimic body states corresponding to the respective affects a person is presented with (Adolphs, 2003; Adolphs et al., 2000). Stronger activation of somatosensory areas observed for individuals high in neuroticism might, thus, reflect a greater reliance of neurotic individuals on “simulation” when faced with tasks of emotion judgment.

Stimulus-driven activity and its modulation by personality traits

Aside from delineating task-related effects, data analysis further sought to evaluate differences in the processing of emotional as relative to neutral prosody as well as processing differences among varying qualities of prosodic emotional information particularly expressions of joy or anger.

Comparisons computed with respect to behavioral measures revealed significantly higher rates of correct identification for neutral and angry as compared to happy prosody, replicating previous findings of an advantage for decoding angry prosody over other emotional categories such as fear, love or happiness (Juslin and Laukka, 2003).

However, arguing against the assumptions of a processing advantage, analyses computed on measures of response times indicated that the processing of angry prosody resulted in significantly slower responses compared to both happy and neutral prosody. In an attempt to explain observed effects, response time differences were re-evaluated using an approach that controlled for differences in stimulus duration among the three prosodic categories. Results revealed that, although effects proved in parts driven by stimulus durations, differences between happy and angry prosody remained significant, suggesting an emotion-specific facilitation of responding that warrants further investigation.

Considering stimulus effects at brain level, enhanced hemodynamic responses to stimuli spoken in an emotional rather than a neutral tone of voice were observed bilaterally within the mid superior temporal cortex (m-STC) with the strongest responses obtained for angry prosody within these structures. Additionally enhanced reactivity to emotional as compared to neutral prosody was revealed within the medial frontal cortex (MFC) as well as the left pre- and postcentral cortex. Increased responsiveness of the m-STC to emotional speech melody has been documented in a variety of previous neuroimaging studies (Ethofer et al., 2009; Grandjean et al., 2005; Wiethoff et al., 2008), and given its stimulus-driven modulation of hemodynamic responses independent of task demands, an involvement of the m-STC particularly in the acoustic analysis of vocal emotional stimuli has been assumed (Ethofer et al., 2009; Wildgruber et al., 2009). Enhanced responses of the MFC, on the other hand, have been related to various aspects of social cognition, a set of processes contributing to successful social interaction (Amodio and Frith, 2006). One such fundamental component of social cognition associated particularly with the activation of anterior subdivisions of the MFC has been described to be “mentalizing” (Amodio and Frith, 2006), a process by which inferences about the mental state of others are made (Frith and Frith, 2006). Reading the minds of our partners of interaction, grasping their desires, feelings and believes, proves to

be crucial to effective social functioning as those mental states determine behavior (Frith and Frith, 2006). Emotional speech melody provides valuable cues as to the psychological states of our fellow human beings and activation of the anterior MFC observed in response to emotional speech melody thus might reflect mentalizing processes triggered by the perception of vocal emotional cues.

Similar to the results obtained for task-related brain activation patterns, stimulus-driven activity appeared to be further modulated by individual differences in neuroticism as personality measures of neuroticism were found to correlate with activity of the left anterior MFC to positive as compared to negative prosody. Bearing in mind the involvement of the anterior MFC in social-cognitive processes, particularly in inferring the mental states of our partners of interaction, observed activation patterns may reflect greater effort to “mentalize” positive emotional states in subjects scoring high on measures of neuroticism. Neuroticism has frequently been associated with advantages in the processing of negative emotional information (Chan et al., 2007; Derryberry and Reed, 1994; Gomez et al., 2002; Reed and Derryberry, 1995). Assuming such an affective bias to selectively facilitate the processing of negative vocal emotional stimuli, positive prosodic stimuli may in comparison impose greater demands on social-cognitive processing. In turn, greater demands on social-cognitive processes in relation with the decoding of emotional vocalizations have been associated with enhanced activation of medial frontal brain areas very similar in location to activation patterns observed in the present study (Szameitat et al., 2010).

However, one would expect the proposed disadvantage in the processing of positive emotions to reveal itself, for instance, in slowed response times to happy as compared to angry stimuli or a response bias towards judging emotions as negative. Yet, behavioral data obtained in the present study reveal no such patterns of performance. Employed correlation analyses yielded no significant relationship between neuroticism and measures of performance. One possible explanation for those negative findings might be that categorical judgment tasks (such as those employed in this study) are not sensitive enough to evaluate biases in the processing of different types of emotions. In order to further explore the idea of a neuroticism-linked processing bias and its cerebral underpinnings, it appears worthwhile to re-evaluate the respective hypothesis using, for instance, tasks that require a continuous rating of the emotional valence of a given speech stimulus.

Particularly in light of lacking behavioral data to support the assumption of a personality-dependent processing bias in the decoding of emotional speech melody, the interpretation of the observed cerebral response patterns at this point remains hypothetical in nature and require further elaboration.

Conclusion

Irrespective of whether observed personality-dependent variations in activation patterns may reflect processing biases, differences in emotion control or task strategies, reported findings, first and foremost, evidence a clear influence of personality on brain responses related to the processing of emotional speech melody.

In highlighting such personality-dependent modulations of brain activation, the present study, again underlines the importance of considering individual differences in the study of prosody processing and encourages to further elaborate the effects of such differences in order to broaden our insight into the neurobiology of prosody perception.

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