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Chapter 2.4

Selective automatic activation of the superior temporal gyrus for the perception of angry prosody

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Abstract

Significant progress has been made in delineating the neural network involved in the perception of emotional prosody. However, it is still unclear to what extent there is differential involvement of neural structures in the intentional (explicit) vs. unintentional (implicit) perception of emotional prosody. Further, it is unknown whether automaticity of emotional prosody perception found in previous investigations is specific for threatening prosody or a general property of emotional prosody perception. Therefore, in the present study we used functional magnetic resonance imaging to investigate the neural networks involved in the intentional and unintentional perception of surprise and anger prosody. The core temporofrontal prosody perception network was found to be active independently of instruction, in line with recent models of emotional prosody perception. For explicit emotional prosody perception, additional activation was found in areas previously implicated in 'Theory of Mind' processing. Hemispheric specialization within the core emotional prosody perception network showed a rightward asymmetry for implicit prosody, but shifted to symmetric activation during explicit prosody perception, showing that hemispheric asymmetry for emotional prosody perception is relative and can be modulated by task demands only. Last, persistent supra-threshold activation of the right superior temporal gyrus was found for unintentional perception of anger but not for surprise, supporting models that postulate phylogenetically prepared prioritized processing of threat signals in the brain.

1. Introduction

Accurate perception of non-verbal emotional signals is essential for social interactions. Through the voice, the emotional state of the speaker can be conveyed by means of prosody (the suprasegmental layer of speech), using various acoustic parameters such as speaking rate, fundamental frequency and spectral balance (e.g., Van Heuven & Sluijter 1996; Scherer, 2003). It can be argued that in every-day life most emotional cues are processed spontaneously and only in exceptional situations do we deliberately evaluate the emotional state of the speaker through decoding of non-verbal signals (Critchley et al., 2000). Thus, implicit perception of emotional prosody may represent the rule and explicit perception the exception. The present investigation examined the neural network underlying implicit versus explicit perception of emotional prosody.

Neural models of emotional prosody perception (Kotz & Paulmann, 2011; Bruck et al., 2011; for meta-analytic evidence see Witteman, Van Heuven, & Schiller, 2012) have proposed that emotional meaning is extracted from the speech signal in three stages. First, extraction of basic acoustic properties from the speech signal takes place in the primary and secondary auditory cortex, i.e., Heschl's gyrus (HG) and the mid-superior temporal gyrus (mid STG), where the terms 'anterior', 'mid' and 'posterior' STG will henceforth be used relative to the location of HG (i.e., 'mid' lies parallel to HG, see Turkeltaub, Branch, & Coslett, 2010). Further, both models propose that in a second stage these acoustic properties are integrated into an 'emotional gestalt', but disagree whether its anatomical substrate lies in the posterior STG (Bruck et al., 2011, for meta-analytic support of this model, see Witteman et al., 2012) or anterior STS (Kotz & Paulmann, 2011). Last, both models propose a third stage, in which emotional prosody is evaluated and integrated with other layers of speech (such as the lexico-syntactic meaning of the utterance) in lateral frontal areas. Additionally, it has been suggested that subcortical areas are involved in emotional prosody perception such as the amygdala and basal ganglia (for reviews see Kotz & Paulmann, 2011; Bruck et al., 2011). However, upon closer inspection, the amygdala may not be essential for emotional prosody perception since lesion studies have repeatedly failed to find compromised emotional prosody perception after amygdala damage (Adolphs & Tranel, 1999; Bach, Hurlemann, & Dolan, 2013). The precise role of the various basal ganglia nuclei in the emotional prosody perception process remains to be determined.

Implicit versus explicit processing of emotional processing may tax the various components of the core prosody perception network differentially. Additionally, as explicit processing of prosody demands an extra stage of information processing as compared to implicit emotional prosody processing, additional areas may be recruited during explicit processing. Previous neuroimaging studies have examined this issue in two ways. First, by comparing a condition in which participants actively evaluate emotional prosody with a condition where subjects evaluate a different dimension of the same stimuli (such as gender identification), the components of the explicit emotional prosody perception network can be extracted. These contrasts have generally revealed enhanced processing in the posterior STG and IFG for explicit emotional prosody processing (for meta-analytic evidence, see Witteman, Van Heuven, & Schiller, 2012). Note, however, that these components may additionally reflect other differences between the two tasks used than just the explicit versus implicit processing mode.

Alternatively, this confound can be eliminated by comparing emotional prosody vs. neutral prosody perception under an explicit condition to the same stimulus-driven contrast under an implicit processing condition (Frühholz, Ceravolo, &

Grandjean, 2012). When qualitatively comparing studies using such a stimulus-driven contrast under an explicit condition (Kotz et al., 2003; Leitman et al., 2010; Frühholz et al., 2012) with studies that used a stimulus-driven task under an implicit processing condition (Grandjean et al., 2005; Sander et al., 2005; Frühholz et al., 2012; Mothes-Lasch, Mentzel, Miltner, & Straube, 2011) the explicit studies sometimes find involvement of the middle temporal gyrus MTG (Leitman et al., 2010) and the temporoparietal junction (Frühholz et al., 2012), while the implicit studies do not. Interestingly, the MTG and temporoparietal junction (TPJ) have been suggested to be involved in ‘Theory of Mind’ (ToM) processing in the previous literature (Bzdok et al., 2012) and may therefore be part of an extended emotional prosody perception network for deliberate (explicit) analysis of non-verbal emotional information. Crucially, the only two studies that have compared explicit to implicit processing directly using stimulus-driven contrasts, suggest involvement of the anterior cingulate and the putamen in explicit processing of emotional prosody (Bach et al., 2008; Frühholz et al., 2012). Thus, in the present investigation we similarly contrasted explicit and implicit processing of a stimulus-driven contrast to examine which regions of the emotional prosody perception network are involved in implicit and explicit processing of emotional prosody.

It has been suggested that emotional processing might be relatively ‘automatic’ (Anderson, Christoff, Panitz, De Rosa, & Gabrieli, 2003; Sander et al., 2005, for a recent review see Straube, Mothes-Lasch & Miltner, 2011) and that such automaticity might reflect a phylogenetically prepared mechanism for biologically relevant stimuli to get privileged access to the limited processing capacity of the brain (Öhman & Mineka, 2001) due to selective pressure for processing of emotional signals in evolutionary history (Dunbar, 1998; Silk, 2007). Upon closer examination, the terms ‘implicit’ and ‘automatic’ overlap to such an extent that it has been argued that we can replace the former with the latter, as the latter is better defined (Moors & De Houwer, 2006). According to Moors and De Houwer, automaticity is a gradual concept that comprises several core features such as uncontrollability, efficiency and lack of awareness of the process – the more of these features are present the more ‘automatic’ a process can be considered to be. One aspect of the uncontrollability aspect of automaticity is whether a process is initiated even when the subject does not have the goal to initiate the process (i.e., unintentionally of emotional processing). Thus, in the present investigation we examined whether emotional prosody processing persists despite lack of the participant’s intention to engage in emotional prosody processing. On the neural level, we defined the persistence of emotional prosody processing as the continued presence of supra-threshold neural activity during unintentional emotional prosody perception, as compared to intentional emotional prosody processing (similarly to Anderson et al., 2003).

Finally, it has been suggested that there might have been particular selective pressure for automatic processing of negative emotions and more specifically threat (e.g., anger) since rapid threat detection can prevent harm to the organism and this promote fitness (Öhman & Mineka, 2001; Anderson, Christoff, Panitz, De Rosa, & Gabrieli, 2003; Schupp et al., 2004). Indeed, some evidence for automaticity of the perception of threatening (i.e. anger) prosody has been found previously (Sander et al., 2005; Grandjean et al., 2005). Further, there is evidence from the visual modality that negative emotional signals in particular attract additional processing resources (Holmes, Bradley, Kragh, Nielsen, & Mogg, 2009; Ito, Larsen, Smith, & Cacioppo, 1998; Schupp et al. 2004; but for conflicting evidence see Schröder et al., 2006) as compared to

positive emotional stimuli. Thus, processing of threat may be relatively automatic as compared to processing non-threatening emotional information. To test this hypothesis, it is required to examine whether the persistence of neural activity under unintentional emotional processing is particularly evident for negative emotions as compared to positive emotions, which has not been examined for emotional prosody yet. Thus, as a last goal of the present investigation, we examined the persistence of supra-threshold neural activity during task-irrelevant processing of positive versus negative (threatening) emotional prosody.

2. Methods

2.1. Participants

A total of 25 participants took part in the experiment. Five participants were excluded because of lower than chance level performance and one more due excessive motion (average displacement > 2.5 mm), resulting in a total of 19 participants (mean age 24.92, SD = 5.65; 6 male, 13 female). All participants were right-handed as determined by the Edinburgh Handedness Inventory (M = 88.11, SD = 11.32, minimum = 67), were native speakers of Dutch, had normal or corrected-to-normal vision and no current psychiatric disorder or a history of neurological disease. Furthermore, none of the participants reported hearing problems or substance dependence. The study was approved by the local ethics committee and conducted in accordance with the Declaration of Helsinki, and informed consent was obtained from all participants prior to the experiment. Participants received € 20 for their participation in the two hour fMRI session.

2.2. Materials

Pseudowords (see appendix A) with a disyllabic structure were generated. All pseudowords obeyed Dutch phonotactics and were checked for the absence of semantic content. All pseudowords were expressed with neutral, (pleasantly) surprised and angry prosody and with stress either on the first or second syllable by two professional actors (one male, one female) and recorded at 16 bit resolution and a 44.1 kHz sampling rate in a sound-proofed booth. Surprised and angry prosody were chosen in order to sample both positive and negative emotions - both of which are considered to be approach emotions (thus, there was no confounding role of the approach-withdrawal dimension). Items were intensity-normalized and had a mean duration of 756 ms (SD = 65 ms).

In line with previous literature (e.g., Scherer, 2003), the emotional categories differed from neutral prosody in mean F_0 and F_0 variability; anger differed additionally in intensity variability (see Table 1). Note that the three categories did not differ in mean intensity as the stimuli had been intensity-normalized. To verify the validity of the intended prosodic contrasts, a panel of five healthy volunteers classified each prosodic stimulus (in addition to happy and sad prosodic stimuli that were not used in the present study) in a forced choice task. Only pseudowords were selected for which all of the emotional prosodic categories (neutral, surprised and angry intonation) were classified correctly by at least 4 out of 5 panel members for both actors.

Two categorization tasks were created that presented identical stimuli under an implicit and explicit emotional condition. For the *explicit* (intentional) emotional condition, participants were instructed to decide whether the stimulus sounded neutral,

angry or surprised. For the *implicit* (unintentional) emotional task participants were required to categorize a non-emotional dimension of the same stimuli (whether metrical stress was on the first or the second syllable). From the pool of validated stimuli, 32 items of each emotional category were selected, with half of the words bearing metrical stress on the first and the other half on the second syllable. Speaker gender was balanced across all items.

Table 1. Acoustic properties of the emotional categories.

	Neutral	Anger	Surprise
Mean intensity (dB)	79.45	79.27	80.64
Mean variation (SD) intensity	8.84	10.74	8.83
Mean F₀ (Hz)	180.73	281.35	282.46
Mean variation (SD) F₀	44.78	78.56	101.19
Mean total duration (s)	0.79	0.76	0.72

2.3. Procedure

Each participant performed both tasks, each of which took 12 minutes to complete. The implicit emotional task was always presented first to reduce participants' awareness of the emotional dimension of the stimuli (and hence to prevent intentional processing of emotional prosody, allowing us to investigate the intentionality dimension of automaticity in emotional prosody perception (see Moors & De Houwer, 2006). Participants were instructed that they would hear a nonsense word and asked to categorize the task-relevant dimension (emotion, metrical stress) as fast and accurately as possible with a right hand button press. Assignment of individual categories to response buttons was counterbalanced across subjects. Participants were instructed that they could respond while the stimulus was still playing (i.e., reaction times [RTs] were recorded from the onset of the stimulus). All other instructions were exactly the same for both tasks except for words describing the task-specific (emotional versus non-emotional) categories.

Each categorization task started with 12 practice trials. Participants practised the tasks in the scanner with simulated scanner noise and kept practising until a performance level of at least 75% correct was reached. Subsequently, the 96 test trials (32 items per emotional category) were performed.

Throughout the experiment a black fixation cross was presented in the center of a grey background. Auditory stimuli were presented binaurally through MR-compatible headphones and a trial ended 2000 ms after stimulus onset. Stimuli were presented in an event-related fashion with a jittered inter stimulus interval (between 4000 and 8000 ms). Stimulus presentation order was (pseudo-)random with the restriction that no more than two consecutive presentations of the same stimulus category were allowed. Participants were instructed to fix their gaze on the fixation cross throughout the experiment.

Stimulus presentation was controlled using E-prime 1.2 and stimulus material was presented at 16 bit resolution and a 44.1 kHz sampling frequency at a comfortable intensity level. Subjects reported that the stimuli could be perceived clearly despite of the scanner noise.

2.4. fMRI data acquisition

Imaging data were acquired on a Philips 3.0-T Achieva MRI scanner using an eight-channel SENSE head coil for radiofrequency transmission and reception (Philips Medical Systems, Best, The Netherlands). For each task, whole-brain fMRI data were acquired using T_2^* -weighted gradient-echo echo-planar imaging (EPI) with the following scan parameters: 355 volumes (the first 5 volumes were discarded to reach signal equilibrium); 38 axial slices scanned in ascending order; repetition time (TR) = 2200 ms; echo time (TE) = 30 ms; flip angle = 80° ; FOV = 220×220 mm; 2.75 mm isotropic voxels with a 0.25 mm slice gap. A high-resolution anatomical image (T_1 -weighted ultra-fast gradient-echo acquisition; TR = 9.75 ms; TE = 4.59 ms; flip angle = 8° ; 140 axial slices; FOV = 224×224 mm; in-plane resolution $.875 \times .875$ mm; slice thickness = 1.2 mm), and a high-resolution T_2^* -weighted gradient echo EPI scan (TR = 2.2 s; TE = 30 ms; flip angle = 80° ; 84 axial slices; FOV = 220×220 mm; in-plane resolution 1.96×1.96 mm, slice thickness = 2 mm) were additionally acquired for registration to standard space.

2.5. fMRI data preprocessing

Prior to analysis, all fMRI data sets were submitted to a visual quality control check to ensure that no gross artefacts were present in the data. Next, data were analyzed using FSL Version 4.1.3 (Smith et al., 2004). The following preprocessing steps were applied to the EPI data sets: motion correction, removal of non-brain tissue, spatial smoothing using a Gaussian kernel of 8 mm full width at half maximum (FWHM), grand-mean intensity normalization of the entire 4D dataset by a single multiplicative factor, and a high pass temporal filter of 70s (i.e., ≈ 0.014 Hz). The dataset was registered to the high resolution EPI image, the high resolution EPI image to the T1-weighted image, and the T1-weighted image to the 2 mm isotropic MNI-152 standard space image (T1-weighted standard brain averaged over 152 subjects; Montreal Neurological Institute, Montreal, QC, Canada). The resulting transformation matrices were then combined to obtain a native to MNI space transformation matrix and its inverse (MNI to native space).

2.6. Behavioral analysis

Repeated-measures analyses of variance (RM-ANOVA) were performed with Task as within-subject factor and proportion correct responses and mean reaction time for correct responses as dependent variables.

2.7. fMRI-data analysis

2.7.1. Whole brain analyses

Data analysis was performed using FEAT (fMRI Expert Analysis Tool) Version 5.98, part of FSL (FMRIBs Software Library, <http://www.FMRIB.ox.ac.uk/fsl>). In native space, the fMRI time-series was analyzed in an event-related fashion using the General Linear Model with local autocorrelation correction applied (Woolrich, Ripley, Brady, & Smith, 2001). For both runs, onsets of each of the stimulus categories (neutral, angry, surprised) were modeled as events with 800 ms duration in separate regressors. Regressors were convolved with a double gamma hemodynamic response function, and temporal derivatives of each of the three regressors were added to the model. If errors were present, these trials were included in the model with a separate regressor. At first level, every emotional category (neutral, surprise, anger) was contrasted against baseline and against the other emotional categories.

At second level, three whole-brain analyses were performed. First, the main effect of emotional (anger and surprise) versus neutral prosody across both tasks was analyzed to examine the task-independent effect of emotional prosody. Second, the effect of emotional versus neutral prosody was analyzed under the explicit and implicit condition separately to examine activations associated with explicit and implicit emotional prosody perception. Last, the processing of emotional prosody versus neutral prosody was directly compared between the two tasks to examine which brain regions might be specifically engaged during implicit versus explicit emotional prosody perception. All whole-brain analyses were cluster-corrected for multiple comparisons using an initial cluster-forming threshold of $Z > 2.3$ ($p < .01$), and a corrected significance threshold of $p < .05$ (Worsley, 2001) was applied.

2.7.2. Regions of Interest (ROI) analyses

The previous literature suggests that the superior temporal gyrus (STG) and the inferior frontal gyrus (IFG) are particularly important in the perception of emotional prosody (Schirmer & Kotz, 2006; Brück, Kreifelts, & Wildgruber, 2011; Witteman, Van Heuven, & Schiller, 2012). Therefore, the whole-brain analyses were followed up with an a priori region-of-interest (ROI) analysis on the STG and IFG. Anatomical ROIs were created for the IFG (pars opercularis) and STG (posterior part) at the 50% probability threshold, as defined by the Harvard-Oxford cortical probability atlas (<http://www.fmrib.ox.ac.uk/fsl/data/atlas-descriptions.html#ho>). For these ROIs, the mean Z -values were extracted for each stimulus category (anger, surprise, neutral) against baseline and for each emotional category (surprise, anger) against neutral, for each task and each participant using Featquery (<http://fsl.fmrib.ox.ac.uk/fsl/fsl4.0/feat5/featquery.html>). These Z -transformed parameter estimates indicate how well the mean signal of each ROI is explained by the model (i.e., by the presence of the particular stimulus category). Using these mean Z -values as dependent variables, two RM-ANOVAs were performed. First, to examine the effect of prosodic category (anger, surprise, neutral), a RM-ANOVA was performed with the Z -values against baseline as dependent variables and the factors Task, ROI, Hemisphere and Emotion as within-subject factors. Secondly, to specifically examine lateralization effects for emotional prosody an additional RM-ANOVA was performed with the Z -values of each emotional category (anger, surprise) against neutral as dependent variable and the factors Task, ROI, Hemisphere and Emotion as within-subject independents. For this analysis only main effects of and interactions with the factor Hemisphere are reported. In case of sphericity-violations, Greenhouse-Geisser corrected p -values are reported.

3. Results

3.1. Behavioral results

As depicted in Figure 1, participants performed well above chance level for the explicit task ($M = 88\%$, $SD = 7.8\%$) and the implicit task ($M = 83\%$, $SD = 8.5\%$). Furthermore, a RM-ANOVA with the proportion correct responses as dependent variable, Task and Emotion as the within-subject factors revealed a main effect of Task ($F(1,18) = 6.21$, $p = .02$), which was qualified by a Task \times Emotion interaction ($F(2,17) = 10.74$, $p = .001$). Follow up RM-ANOVAs for each task with Emotion as independent variable showed

that there were no significant differences in accuracy between the emotional categories for the explicit task (for all, $p > .08$, Sidak corrected). For the implicit task however, accuracy was lower when the task-irrelevant emotional category was surprise as compared to neutral ($p = .03$, Sidak corrected) and to anger ($p < .001$, Sidak corrected), while there was no difference between anger and neutral ($p = .21$).

A RM-ANOVA with reaction time (RT) for correct categorization as the dependent variable revealed a main effect of Task ($F(1,18) = 4.83$, $p = .04$) with slower responses for the implicit task ($M = 1174$; $SD = 133$) than the explicit task ($M = 1111$; $SD = 100$). Further, there was a main effect of Emotion ($F(1,18) = 19.54$, $p < .001$) which was qualified by a Task \times Emotion interaction ($F(2,36) = 7.81$, $p = .007$). Follow-up RM-ANOVAs for each task, indicated that for the explicit task surprise ($p = .02$, Sidak corrected) and anger ($p < .001$, Sidak corrected) were categorized faster than neutral, while anger and surprise were not significantly different ($p = 0.07$, Sidak corrected). For the implicit task categorization was slower when the task irrelevant emotional category was surprise as compared to neutral ($p = .04$, Sidak corrected) and anger ($p < .001$, Sidak corrected) while there was no difference between neutral and anger ($p = .69$).

In sum, the behavioral results suggest that participants perceived the stimuli well and that performance was better for anger and surprise in the explicit task than neutral, and that performance improved when anger was the task irrelevant emotional category during the implicit task.

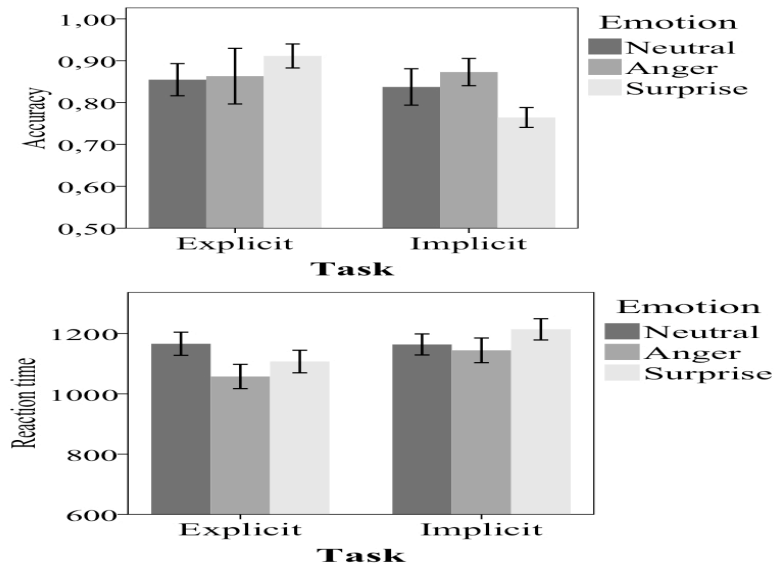


Figure 1. Behavioral results. Mean accuracy (upper graph) and reaction time (lower graph) for each task and each emotional category. Error bars indicate the 95% confidence interval.

3.2. FMRI results

3.2.1. Whole-brain analyses

All effects for the whole-brain analyses can be found in Table 2. The whole-brain cluster-corrected ($p < 0.05$) analysis for [emotion > neutral] across both tasks revealed one cluster with a peak in the right anterior STG/STS (peak MNI coordinates (60, -10, -6), peak $Z = 4.48$, extent = 673 voxels), extending both anteriorly and posteriorly with respect to HG. As shown in Figure 2, additional activation in the left STG and IFG was observed at a more liberal threshold ($p < .001$, uncorrected). For [anger > neutral] the cluster-corrected analysis revealed a cluster with a peak in the right posterior STG/STS (peak MNI coordinates (63, -30, 2), peak $Z = 4.49$, extent = 1215 voxels) and the left mid STG/STS (-54, -22, 0), peak $Z = 4.12$, extent = 326 voxels), extending posteriorly.

As can be observed in Figure 3 [emotion > neutral] for the explicit task revealed a large cluster with a peak in the left mid STS (-58, -26, -4), peak $Z = 3.56$, extent = 1381 voxels), extending into the anterior STG and posterior MTG. A second cluster was observed in the left temporoparietal junction (TPJ) with a peak in the supramarginal gyrus (-52, -54, 32), peak $Z = 3.75$, extent = 1131 voxels), extending into the angular gyrus and the posterior STG. As can be seen in Figure 4 contrasting anger against neutral [anger > neutral] revealed a cluster with a peak in the right posterior STS (60, -30, 0), peak $Z = 3.6$, extent = 1250 voxels), extending into the STG anteriorly and posteriorly with respect to HG. Contrasting surprise to neutral [surprise > neutral] revealed a large cluster with a peak in the left posterior MTG (-60, -54, -2), peak $Z = 3.81$, extent = 2579 voxels), extending anteriorly into the MTG/STS/STG and dorsally into TPJ.

For the implicit task, contrasting both emotional categories to neutral did not reveal any significant clusters. However, as can be seen in Figure 4, contrasting anger to neutral [anger > neutral] revealed a large cluster with a peak in the right mid STG/STS (70, -24, 4), peak $Z = 3.54$, extent = 1351 voxels), extending both anteriorly and posteriorly along the STG/STS. As can be observed in Figure 4 this cluster overlapped to a considerable extent with the cluster found for anger processing in the explicit condition. Lastly, contrasting surprise to neutral [surprise > neutral] resulted in a cluster with a peak in the medial SFG (0, 12, 58), peak $Z = 3.59$, extent = 99 voxels), extending ventrally into the cingulate gyrus.

Directly contrasting emotional prosody processing (versus neutral) in the explicit task with processing of the same emotional categories in the implicit condition (and vice versa) did not reveal any significant clusters of activation.

In sum, the whole-brain analysis indicated that parts of the left and right STG were involved in emotional prosody perception. For the explicit task, TPJ was additionally activated and surprise activated the left MTG during the explicit task and the medial SFG in the implicit task. Interestingly, anger activated the right STG during both tasks while surprise did not. Lastly, no area was significantly more active during emotional prosody perception in the implicit task as compared to the explicit task or vice versa.

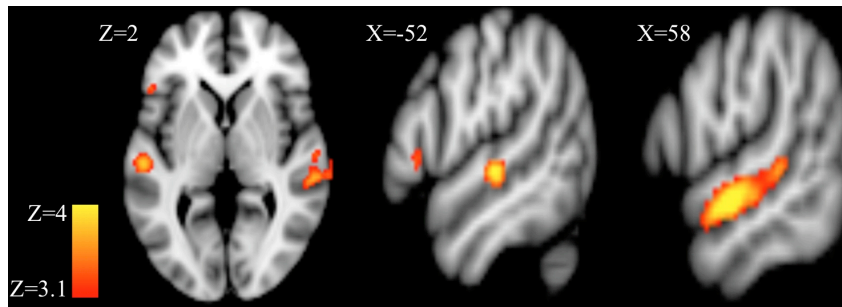


Figure 2. Activation map for emotional > neutral prosody across tasks overlaid on the MNI standard brain. Activation is thresholded at $p < .001$ uncorrected for illustration purposes. The left and right side of the image represent the left and right side of the brain.

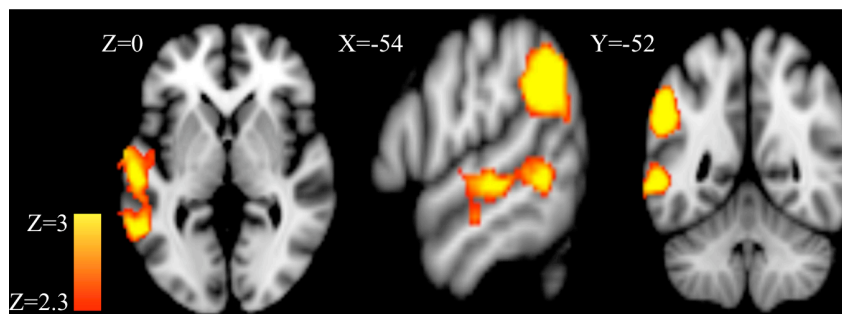


Figure 3. Activation clusters for emotional > neutral in the explicit task overlaid on the MNI standard brain. Clusters of significant activation ($p < .05$, cluster corrected) were observed in the left mid-STS (extending into the anterior STG and posterior MTG) and left TPJ (cluster peak in the supramarginal gyrus).

Table 2. Peak activations for the whole brain analyses.

Effect	Contrast	Brain region (peak)	Peak MNI (x,y,z)	Z-value	Cluster size in voxels
<i>Main effect</i>	[Emotion > neutral]	R STG	60, -10, -6	4.48	673
	[Anger > neutral]	R STG; L STG	63, -30, 2; -54, -22, 0	4.49; 4.12	1215; 326
<i>Explicit task</i>	[Emotion > neutral]	L STG; L SMG;	-58, -26, -4; -52, -54, 32	3.56; 3.75	1381; 1131
	[Anger > neutral]	R STG	60, -30, 0	3.6	1250
	[Surprise > neutral]	L MTG	-60, -54, -2	3.81	2579
<i>Implicit task</i>	[Anger > neutral]	R STG	70, -24, 4	3.54	1351
	[Surprise > neutral]	M SFG	0, 12, 58	3.59	999

L=left, R=Right, M=midline. STG=superior temporal gyrus, MTG = middle temporal gyrus, SFG = superior frontal gyrus, SMG = supramarginal gyrus. Coordinates are given in Montreal Neurological Institute (MNI) standard space. All reported clusters survive a $p < 0.05$ cluster correction.

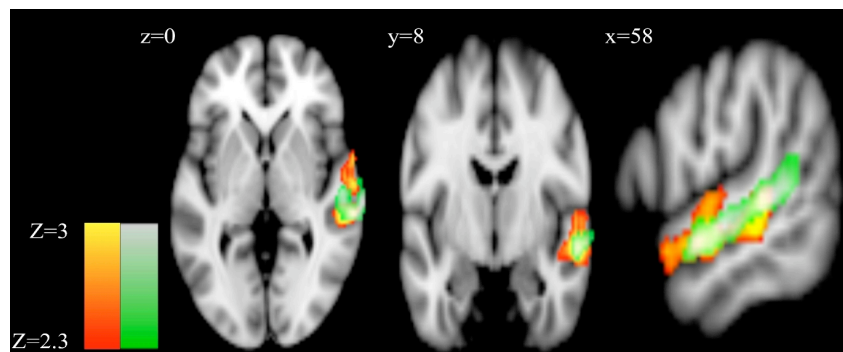


Figure 4. Activation clusters for anger > neutral in the explicit task (red to yellow) and the implicit task (green to white). A significant cluster of activation ($p < .05$, cluster corrected) was found in the right STG/STS for both tasks, but activation extended more anteriorly for the explicit task and more posteriorly for the implicit task.

3.2.2. ROI-analyses

ROI analyses were performed to further characterize the effect of emotional prosody in the core temporofrontal network, including the STG and IFG, which was robustly associated with emotional prosody perception in previous studies. The mean Z-values for each ROI in each condition against baseline are shown in Figure 5. A RM-ANOVA with Task, ROI, Hemisphere and Emotion as within-subject factors and the Z-values against baseline as dependent variables revealed a main effect of Task ($F(1,18) = 12.89$, $p = .002$), ROI ($F(1,18) = 53.66$, $p < .001$), Hemisphere ($F(1,18) = 6.01$, $p = .02$) and Emotion ($F(1,18) = 4.04$, $p = .04$). The Task, ROI and Emotion main effects were qualified by a three-way Task \times ROI \times Emotion interaction ($F(1,17) = 21.46$, $p < .001$). Decomposing the interaction with separate RM-ANOVAs for each ROI revealed a significant Task \times Emotion interaction for the STG ($F(2,36) = 4.47$, $p = .04$) but not for the IFG ($p = .12$). Following the interaction up for the STG with separate RM-ANOVAs for each task revealed a main effect of Emotion in the explicit task ($F(1,18) = 7.63$, $p = 0.003$) and in the implicit task ($F(1,18) = 10.66$, $p = .001$) for the STG. Post-hoc tests (Sidak corrected) indicated that for the explicit task, both anger ($p = .03$) and surprise ($p = .004$) activated the STG more than neutral while anger and surprise were not significantly different ($p = 1$, NS). For the implicit task, anger activated the STG more than neutral ($p = .002$) and surprise ($p = .01$) while surprise and neutral were not significantly different ($p = .91$, NS).

To further characterize lateralization effects of emotional prosody, the Z-score of each emotion (anger, surprise) against the neutral condition was used as dependent variable. The analysis revealed a Task \times Hemisphere interaction ($F(1,18) = 5.86$, $p = .03$) and a ROI \times Hemisphere \times Emotion interaction ($F(1,18) = 5.41$, $p = .03$). Following up the Task \times Hemisphere interaction with a separate ANOVA for each task, revealed that for the explicit task there was no significant difference between the hemispheres ($p = .39$, NS) while for the implicit task right-hemispheric activation was significantly larger than left-hemispheric activation ($F(1,18) = 6.39$, $p = .02$). However, in the uncorrected statistical map significant activity was noted in the left STG, showing that the right-hemispheric advantage was relative. Decomposing the ROI \times Hemisphere \times Emotion interaction with separate ANOVAs for each ROI did not reveal a significant Hemisphere \times Emotion interaction for the STG ($F(1,18) = .34$, $p = .57$) but a significant Hemisphere \times Emotion interaction in the IFG ($F(1,18) = 7.57$, $p = .01$). Follow up RM-ANOVAs for each emotional category revealed a trend for a right-hemispheric advantage for anger in the IFG ($F(1,18) = 4.15$, $p = .06$) but no difference between the hemispheres for surprise ($F(1,18) = 1.57$, $p = .23$).

In sum, the ROI analyses suggest that the bilateral STG was sensitive to both emotional categories (versus neutral) when attention was directed at the emotional prosody. However, when attention was diverted away from the emotional prosodic dimension during the implicit task, only anger maintained more activation than neutral in the STG while surprise did not. Thus, diverting attention away from the emotional prosody decreased processing of surprise as compared to neutral below the statistical significance threshold (although the decrease in activation between tasks was not significant) in the STG, while above-threshold activation for anger processing was sustained. Lastly, we found a modulation of hemispheric asymmetry by task demands in the temporofrontal network, with bilateral activation for emotional (against neutral) prosody in the explicit task and relative right lateralization in the implicit task.

Therefore, the unilateral activation clusters found for the whole-brain analyses in the STG seem largely due to thresholding effects.

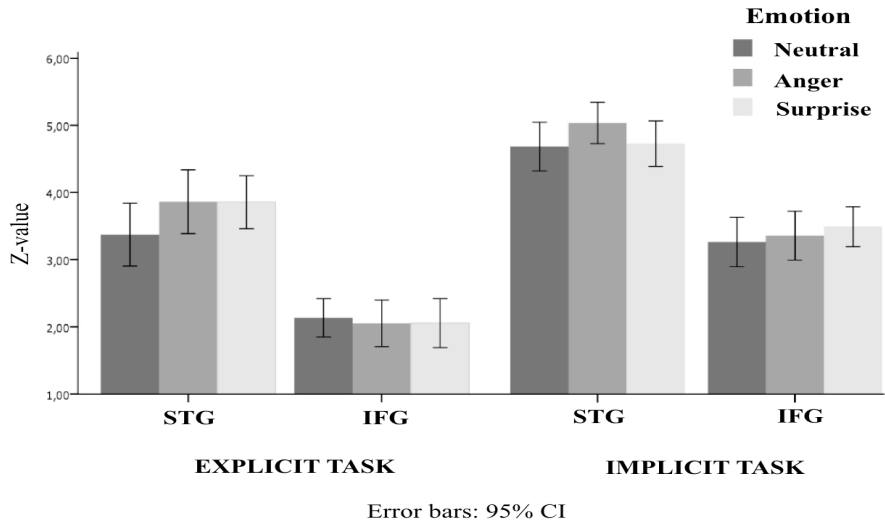


Figure 5. The mean Z-value for each task and each emotion is shown for the IFG and the STG. Error bars indicate the 95% confidence interval.

4. Discussion

The aim of the present study was to investigate the brain areas involved in the implicit (unintentional) and explicit (intentional) perception of emotional prosody. Further, it was investigated whether automaticity for emotional prosody processing could be demonstrated, and if so, whether it might be particularly evident for anger. First, we found activation of the core temporofrontal prosody perception network (comprising the STG and IFG) independently of task demands. Further, for explicit perception of emotional prosody additional activation was found in the left middle temporal gyrus, angular gyrus and the supramarginal gyrus. However, comparing both tasks directly for both emotions against neutral revealed no differential activation between both modes of processing. Last and importantly, anger processing showed sustained supra-threshold activation of the right STG under both task conditions while surprise only showed supra-threshold STG activation in the explicit condition.

In line with recent models of emotional prosody perception (Kotz & Paulmann, 2011; Brück, Kreifelts, & Wildgruber, 2011) and meta-analytic evidence (Witteman, Van Heuven, & Schiller, 2012), activation was found along the STG/STS for stimulus driven (i.e., emotion contrasted against neutral) emotional prosody perception and additionally in the IFG (uncorrected) independently of task demands. Thus, this result adds to the growing evidence base in support of a core temporofrontal network that is involved in the (at least) three stage emotional prosody perception process, involving extraction of acoustic features relevant to emotional prosody, integration of those features into more abstract representations and finally evaluation of these representations and integration with other layers of the speech signal.

Our results further suggest that intentional processing of emotional prosody may recruit additional areas beyond the core emotional prosody perception network. During intentional emotional prosody perception, additional activation was found in the left MTG and the left TPJ extending into the supramarginal and angular gyrus, while during unintentional (implicit) emotional prosody processing these areas were not significantly activated (however these areas were not more active during the explicit task as compared to the implicit task). Involvement of the MTG or TPJ in intentional emotional prosody perception has been observed in previous work (Wildgruber, Pihan, Ackermann, Erb, & Grodd, 2002; Ethofer et al., 2009; Leitman et al., 2010; Frühholz et al., 2012, but see Kotz et al., 2003) and within the context of emotional processing the MTG has been suggested to be involved in abstract multimodal processing of emotion (Mitchell, Elliott, Barry, Cruttenden, & Woodruff, 2003; Pourtois, De Gelder, Bol, & Crommelinck, 2005; Johnstone, Van Reekum, Oakes, & Davidson, 2006). Further, a recent meta-analysis (Bzdok et al., 2012) of the neuroimaging literature suggests that the MTG and TPJ play a key role in ‘Theory of Mind’, the ability to contemplate about others’ thoughts and feelings in an abstract manner. Thus, the MTG and TPJ may be optionally recruited in addition to the core emotional prosody perception network for more abstract and intentional analysis of others’ feelings as communicated through the voice. However, the involvement of these additional structures during intentional prosody perception may be a matter of degree rather than type, as the direct statistical comparison between both tasks did not reveal any clusters differentiating between both tasks. Further, although admittedly this is accepting the null hypothesis, the direct comparison between the two tasks suggests that the core prosody perception network is also similarly active during intentional (explicit) and unintentional (implicit) emotional prosody perception.

Regarding hemispheric specialization for emotional prosody perception, previous meta-analytic evidence has suggested that there is relative right-hemispheric specialization (Witteman, Van IJzendoorn, Van de Velde, Van Heuven, & Schiller, 2011) that might be driven by relatively early specialization for the processing of acoustic cues relevant to emotional prosody perception (such as F_0) in the primary and secondary auditory cortex (Witteman, Van Heuven, & Schiller, 2012). Although in the present study the whole brain analysis for task independent effects revealed a cluster in the right STG, inspection of the uncorrected activation maps revealed bilateral activation in the STG. Further, ROI analysis of the STG and IFG showed overall bilateral activation independent of task, bilateral activation during the explicit task and relatively greater activation in the right than the left hemisphere during implicit (unintentional) emotional prosody perception. A problem with interpreting the previous neuroimaging evidence regarding hemispheric specialization for emotional prosody perception is that most studies do not perform a formal statistical test for lateralization and only report (lateralized) clusters of supra-threshold activation. With this approach the possibility cannot be excluded that in reality there is no meaningful difference in activity between the hemispheres. Indeed, previous neuroimaging studies that did perform a formal test of hemispheric lateralization either found no hemispheric asymmetry (Grandjean et al., 2005) or relative right hemispheric asymmetry to bilateral activation, depending on the specific emotional category analyzed (Leitmann et al., 2010). Thus, in line with these studies and meta-analytic work (Witteman et al., 2011; Witteman et al., 2012), our results suggest that right hemispheric specialization for emotional prosody perception is relative at best. Further, in accordance with previous work (e.g. Luks, Nusbaum, & Levy, 1998; Gandour et al., 2004) the present results suggest that the hemispheric asymmetry during prosody perception can be modulated by task demands only (as acoustic material was held constant between the tasks), with greater activation of the right hemisphere than the left during implicit emotional prosody perception shifting to symmetric activation during explicit emotional prosody perception. Although speculative, a greater contribution of the left hemisphere during explicit emotional prosody perception might be related to the added verbal load required for verbal labeling of emotional prosody (Ross et al., 1997).

Of note, no significant activation of the amygdala was found in any of the activation maps. Although the amygdala is often claimed to be essential for adequate emotional prosody perception, a recent meta-analysis of the neuroimaging literature of emotional prosody perception did not find significant convergence of activity across studies in the amygdala (Witteman et al., 2012). Further, lesion studies have repeatedly failed to find significant disturbance of emotional prosody perception in patients with amygdala lesions as compared to controls (Adolphs & Tranel, 1999; Adolphs, Tranel, & Damasio, 2001; Bach, Hurlemann, & Dolan, 2013), suggesting that the amygdala might not be necessary for emotional prosody perception. However, it has been suggested that amygdala involvement in the emotional prosody perception process might be hard to detect with a whole brain analysis because there is differential involvement of the various subnuclei (Frühholz et al., 2012) and because the amygdala rapidly habituates to emotional prosody (Wiethof, Wildgruber, Grodd, & Ethofer, 2009; but see Scheuercker et al., 2007), preventing its detection with typical fMRI designs that involve sustained stimulation, as the present.

We were additionally interested in whether automaticity for emotional prosody perception could be demonstrated, and if so, whether automaticity would be

particularly evident for threat processing, as has been predicted on evolutionary grounds (Öhman & Mineka, 2001; Anderson, Christoff, Panitz, De Rosa, & Gabrieli, 2003; Schupp et al., 2004). Building on the conceptual work on automaticity by Moors and De Houwer (2006), we specifically investigated whether the ‘uncontrollability’ aspect of automaticity could be demonstrated for emotional prosody perception – i.e., whether emotional prosody processing would persist even when participants do not intend to initiate the emotional prosodic perception process. On the neural level, we adopted the criterion for automaticity proposed by Anderson et al. (2003) – i.e., the persistence of supra-threshold activation of neural structures during unintentional emotional prosody perception as compared to intentional emotional prosody perception. Indeed, in the present study the right STG remained significantly active when subjects did not intentionally analyze emotional prosody for anger (as compared to neutral) but not for surprise. Activation of the right temporal cortex during unintentional emotional prosody perception has been found previously for anger as compared to neutral prosody (Grandjean et al., 2005; Sander et al., 2005). However, in these previous studies anger was the only emotional prosody category employed, rendering it uncertain the possibility that such automaticity is specific for anger processing or that it may be a general property of emotional prosody perception. Thus, the present results extend this previous work by providing initial evidence that automaticity of emotional prosody perception seems to be specific to threat. Further, the results support models postulating prioritized processing of negative and particularly threatening emotional signals in the brain (i.e., ‘negativity bias’, see Ito, Larsen, Smith, & Cacioppo, 1998), possibly through a phylogenetically prepared mechanism (e.g., Grossman, Striano, & Friederici, 2005; for a seminal review on preparedness of threat perception, see Öhman & Mineka, 2001). However, it should be noted that even for threat perception automaticity of processing is likely to be relative in the sense that if attentional resources are sufficiently depleted, activation during unintentional emotional perception is eventually reduced (Pessoa, McKenna, Gutierrez, & Ungerleider, 2002; Mothes-Lasch, Miltner, & Straube, 2012; for a review on automaticity of emotional processing and its relativity, see Straube, Mothes-Lasch, & Miltner, 2011). Thus, future investigations should investigate whether specific automatic activation for anger prosody can be replicated and persists under further reduced levels of attention.

Strengths and limitations

The present study had comparably high statistical power as compared to previous investigations of implicit and explicit emotional prosody perception (Bach et al., 2008; Frühholz et al., 2012). As has been noted before (Straube, Mothes-Lasch, & Miltner, 2011; Mothes-Lasch, Miltner, & Straube, 2012), research on automaticity of emotional prosody perception is still in its infancy and has so far exclusively relied on negative emotions. Thus, the present study was the first to include a positive emotional category in addition to anger and neutrality under intentional and unintentional emotional prosody perception, allowing for the first time a test of the specificity of automatic activation during threat perception.

Our study also had some limitations. First, the unintentional emotional perception task was always performed first. Therefore, we cannot exclude the possibility that differences between the two tasks may have been influenced by habituation or sensitization effects. However, as the main goal of the present

investigation was to test the specificity of automatic processing of angry prosody, the fixed task order was deemed necessary, as has been suggested in previous work (Bach et al., 2008) in order to minimize intentional emotional prosody processing during the unintentional task. However, we cannot rule out the possibility that participants did intentionally analyze emotional prosody during the unintentional perception task after all. As suggested in previous work, however (Bach et al., 2008), note that if this had been the case, it would have had the net effect of a more conservative estimation of differences between the two tasks. Second, there were two response categories during the implicit task while there were three during the explicit task. Thus, we cannot exclude the possibility that the use of an extra finger during the intentional emotional perception task may have contributed to differences in activation between the two task conditions.

Conclusion

The present study aimed to investigate the brain areas involved in the implicit and explicit perception of emotional prosody. Activation of the core temporofrontal emotional prosody perception network was found independently of task demands, in line with recent models of emotional prosody perception. For intentional (explicit) perception of emotional prosody, additional activation was found in the MTG and TPJ, possibly reflecting abstract and intentional analysis of others' emotions. Direct comparison between the two tasks, however suggested that the same network is active during both intentional and unintentional emotional prosody perception. Further, in line with recent meta-analytic evidence, the present results suggest that there is relative right-hemispheric specialization for emotional prosody perception at best. The results further suggest that hemispheric asymmetry during prosody perception can be modulated by task demands only. Last, significant persistence of supra-threshold activation during unintentional (implicit) emotional prosody perception was found in the right STG for anger but not surprise, supporting evolutionary grounded models that postulate prioritized processing of threat signals in the brain.

5. References

- Adolphs, R., Tranel, D., & Damasio, H. (2001). Emotion recognition from faces and prosody following temporal lobectomy. *Neuropsychology, 15*, 396-404.
- Adolphs, R., & Tranel, D. (1999). Intact recognition of emotional prosody following amygdala damage. *Neuropsychologia, 37*, 1285-1292.
- Anderson, A. K., Christoff, K., Panitz, D., De Rosa, E., & Gabrieli, J. D. E. (2003). Neural correlates of the automatic processing of threat facial signals. *The Journal of Neuroscience, 23*, 5627-5633.
- Bach, D. R., Grandjean, D., Sander, D., Herdener, M., Strik, W. K., & Seifritz, E. (2008). The effect of appraisal level on processing of emotional prosody in meaningless speech. *NeuroImage, 42*, 919-927.
- Bach, D. R., Hurlmann, R., & Dolan, R. J. (2013). Unimpaired discrimination of fearful prosody after amygdala lesion. *Neuropsychologia, 51*, 2070-2074.
- Brück, C., Kreifelts, B., & Wildgruber, D. (2011). Emotional voices in context: A neurobiological model of multimodal affective information processing. *Physics of Life Reviews, 8*, 383-403.
- Bzdok, D., Schilbach, L., Vogeley, K., Schneider, K., Laird, A., Langner, R., & Eickhoff, S. (2012). Parsing the neural correlates of moral cognition: ALE meta-analysis on morality, theory of mind, and empathy. *Brain Structure and Function, 217*, 783-796.
- Critchley, H., Daly, E., Phillips, M., Brammer, M., Bullmore, E., Williams, S., . . . Murphy, D. (2000). Explicit and implicit neural mechanisms for processing of social information from facial expressions: A functional magnetic resonance imaging study. *Human Brain Mapping, 9*, 93-105.
- Dunbar, R. I. M. (1998). The social brain hypothesis. *Evolutionary Anthropology: Issues, News, and Reviews, 6*, 178-190.
- Ethofer, T., Kreifelts, B., Wiethoff, S., Wolf, J., Grodd, W., Vuilleumier, P., & Wildgruber, D. (2009). Differential influences of emotion, task, and novelty on brain regions underlying the processing of speech melody. *Journal of Cognitive Neuroscience, 21*, 1255-1268.
- Frühholz, S., Ceravolo, L., & Grandjean, D. (2012). Specific brain networks during explicit and implicit decoding of emotional prosody. *Cerebral Cortex, 22*, 1107-1117.
- Gandour, T., Tong, Y., Wong, D., Talavage, T., Dziedzic, M., Xu, . . . Lowe, M. (2004). Hemispheric roles in the perception of speech prosody. *NeuroImage, 23*, 344-357.
- Grandjean, D., Sander, D., Pourtois, G., Schwartz, S., Seghier, M. L., Scherer, K. R., & Vuilleumier, P. (2005). The voices of wrath: Brain responses to angry prosody in meaningless speech. *Nature Neuroscience, 8*, 145-146.
- Grossmann, T., Striano, T., & Friederici, A. D. (2005). Infants' electric brain responses to emotional prosody. *Neuroreport, 16*, 1825-1828.
- Holmes, A., Bradley, B. P., Kragh Nielsen, M., & Mogg, K. (2009). Attentional selectivity for emotional faces: Evidence from human electrophysiology. *Psychophysiology, 46*, 62-68.

- Ito, T. A., Larsen, J. T., Smith, N. K., & Cacioppo, J. T. (1998). Negative information weighs more heavily on the brain: The negativity bias in evaluative categorizations. *Journal of Personality and Social Psychology*, *75*, 887-900.
- Johnstone, T., Van Reekum, C. M., Oakes, T. R., & Davidson, R. J. (2006). The voice of emotion: an fMRI study of neural responses to angry and happy vocal expressions. *Social Cognitive and Affective Neuroscience*, *1*, 242-249.
- Kotz, S. A., Meyer, M., Alter, K., Besson, M., von Cramon, D. Y., & Friederici, A. D. (2003). On the lateralization of emotional prosody: An event-related functional MR investigation. *Brain and Language*, *86*, 366-376.
- Kotz, S. A., & Paulmann, S. (2011). Emotion, Language, and the Brain. *Language and Linguistics Compass*, *5*, 108-125.
- Leitman, D. I., Wolf, D. H., Ragland, J. D., Laukka, P., Loughhead, J., Valdez, J. N., . . . Gur, R. C. (2010). "It's not what you say, but how you say it": A reciprocal temporo-frontal network for affective prosody. *Frontiers in Human Neuroscience*, *4*, 19.
- Luks, T. L., Nusbaum, H. C., & Levy, J. (1998). Hemispheric involvement in the perception of syntactic prosody is dynamically dependent on task demands. *Brain and Language*, *65*, 313-332.
- Mitchell, R. L. C., Elliott, R., Barry, M., Cruttenden, A., & Woodruff, P. W. (2003). The neural response to emotional prosody, as revealed by functional magnetic resonance imaging. *Neuropsychologia*, *41*, 1410-1421.
- Moors, A., & De Houwer, J. (2006). Automaticity: A theoretical and conceptual analysis. *Psychological Bulletin*, *132*, 297-326.
- Mothes-Lasch, M., Mentzel, H. J., Miltner, W. H. R., & Straube, T. (2011). Visual attention modulates brain activation to angry voices. *The Journal of Neuroscience*, *31*, 9594-9598.
- Öhman, A., & Mineka, S. (2001). Fears, phobias, and preparedness: Toward an evolved module of fear and fear learning. *Psychological Review*, *108*, 483-522.
- Pessoa, L., McKenna, M., Gutierrez, E., & Ungerleider, L. G. (2002). Neural processing of emotional faces requires attention. *Proceedings of the National Academy of Sciences*, *99*, 11458-11463.
- Pourtois, G., De Gelder, B., Bol, A., & Crommelinck, M. (2005). Perception of facial expressions and voices and of their combination in the human brain. *Cortex*, *41*, 49-59.
- Ross, E. D., Thompson, R. D., & Yenkosky, J. (1997). Lateralization of affective prosody in brain and the callosal integration of hemispheric language functions. *Brain and Language*, *56*, 27-54.
- Sander, D., Grandjean, D., Pourtois, G., Schwartz, S., Seghier, M. L., Scherer, K. R., & Vuilleumier, P. (2005). Emotion and attention interactions in social cognition: Brain regions involved in processing anger prosody. *NeuroImage*, *28*, 848-858.
- Scherer, K. R. (2003). Vocal communication of emotion: A review of research paradigms. *Speech Communication*, *40*, 227-256.
- Scheurecker, J., Frodl, T., Koutsouleris, N., Zetzsche, T., Wiesmann, M., Kleemann, A. M., . . . Meisenzahl, E. M. (2007). Cerebral differences in explicit and implicit emotional processing--an fMRI study. *Neuropsychobiology*, *56*, 32-39.
- Schröder, C., Möbes, J., Schütze, M., Szymanowski, F., Nager, W., Bangert, M., . . . Dengler, R. (2006). Perception of emotional speech in Parkinson's Disease. *Movement Disorders*, *21*, 1774-1778.

- Schupp, H. T., Öhman, A., Junghöfer, M., Weike, A. I., Stockburger, J., & Hamm, A. O. (2004). The facilitated processing of threatening faces: An erp analysis. *Emotion, 4*, 189-200.
- Shtyrov, Y., Kujala, T., Lyytinen, H., Kujala, J., Ilmoniemi, R. J., & Näätänen, R. (2000). Lateralization of speech processing in the brain as indicated by mismatch negativity and dichotic listening. *Brain and Cognition, 43*, 392-398.
- Silk, J. B. (2007). Social components of fitness in primate groups. *Science, 317*, 1347-1351.
- Smith, S. M., Jenkinson, M., Woolrich, M. W., Beckmann, C. F., Behrens, T. E. J., Johansen-Berg, H., . . . Matthews, P. M. (2004). Advances in functional and structural MR image analysis and implementation as FSL. *NeuroImage, 23*, S208-S219.
- Straube, T., Mothes-Lasch, M., & Miltner, W.H. (2011). Neural mechanisms of the automatic processing of emotional information from faces and voices. *British Journal of Psychology, 102*, 830-848.
- Turkeltaub, P. E., & Branch Coslett, H. (2010). Localization of sublexical speech perception components. *Brain and Language, 114*, 1-15.
- Van Heuven, V. J., & Sluijter, A. M. (1996). Notes on the phonetics of word prosody. In R. Goedemans, E. Van der Hulst, & E. Visch. (Eds.). *Stress patterns in the world, part 1: Background* (233-269). The Hague: Holland Institute of Generative Linguistics, Leiden/Holland Academic Graphics.
- Wiethoff, S. W., Wildgruber, D., Grodd, W., & Ethofer, T. (2009). Response and habituation of the amygdala during processing of emotional prosody. *Neuroreport, 20*, 1356-1360.
- Wildgruber, D., Pihan, H., Ackermann, H., Erb, M., & Grodd, W. (2002). Dynamic brain activation during processing of emotional intonation: Influence of acoustic parameters, emotional valence, and sex. *NeuroImage, 15*, 856-869.
- Witteman, J., Van Heuven, V. J., & Schiller, N. O. (2012). Hearing feelings: A quantitative meta-analysis on the neuroimaging literature of emotional prosody perception. *Neuropsychologia, 50*, 2752-2763.
- Witteman, J., Van Ijzendoorn, M. H., Van de Velde, D., Van Heuven, V. J., & Schiller, N. O. (2011). The nature of hemispheric specialization for linguistic and emotional prosodic perception: A meta-analysis of the lesion literature. *Neuropsychologia, 49*, 3722-3738.
- Woolrich, M. W., Ripley, B. D., Brady, M., & Smith, S. M. (2001). Temporal autocorrelation in univariate linear modeling of FMRI data. *NeuroImage, 14*, 1370-1386.
- Worsley, K. J. (2001). Statistical analysis of activation images. In P. Jezzard, P. Mathews & S. Smith (Eds.). *Functional MRI: An Introduction to Methods* (251-270). New York: Oxford University Press.

APPENDIX A

Pseudowords used in the experiments:

konpon
dinpil
duldin
kondon
duldun
daldan
paldan
dalpan