

# Neural Substrates of Processing Anger in Language: Contributions of Prosody and Semantics

Brian C. Castelluccio<sup>1</sup> · Emily B. Myers<sup>1,2,3</sup> · Jillian M. Schuh<sup>4</sup> · Inge-Marie Eigsti<sup>1,3</sup>

© Springer Science+Business Media New York 2015

**Abstract** Emotions are conveyed primarily through two channels in language: semantics and prosody. While many studies confirm the role of a left hemisphere network in processing semantic emotion, there has been debate over the role of the right hemisphere in processing prosodic emotion. Some evidence suggests a preferential role for the right hemisphere, and other evidence supports a bilateral model. The *relative* contributions of semantics and prosody to the overall processing of affect in language are largely unexplored. The present work used functional magnetic resonance imaging to elucidate the neural bases of processing anger conveyed by prosody or semantic content. Results showed a robust, distributed, bilateral network for processing angry prosody and a more modest left hemisphere network for processing angry semantics when compared to emotionally neutral stimuli. Findings suggest the nervous system may be more responsive to prosodic cues in speech than to the semantic content of speech.

**Keywords** fMRI · Prosody · Semantics · Emotion

## Introduction

In language, emotions are conveyed through two primary channels: semantics and prosody (Berckmoes and Vingerhoets 2004). *Semantics* captures how abstract symbols (words) map onto meaning; *prosody* refers to pitch, intensity, and durational qualities of speech. Detecting

---

✉ Brian C. Castelluccio  
brian.castelluccio@uconn.edu

<sup>1</sup> Department of Psychological Sciences, University of Connecticut, 406 Babbidge Road, Unit 1020, Storrs, CT 06269-1020, USA

<sup>2</sup> Department of Speech, Language, and Hearing Sciences, University of Connecticut, Storrs, CT, USA

<sup>3</sup> Haskins Laboratories, New Haven, CT, USA

<sup>4</sup> Department of Neurology, Division of Neuropsychology, Medical College of Wisconsin, Milwaukee, WI, USA

a speaker's emotional state, which is central to communication and interpersonal functioning (Ekman 1992) requires decoding semantic meaning and prosodic cues. Rapid processing of anger is especially important given its adaptive relevance (Adolphs 2002).

Researchers have debated the relative contributions of each hemisphere in processing emotional cues in language (Alba-Ferrara et al. 2012). A number of neuroimaging studies have examined affective prosody, but there has been comparatively little work on neural substrates of affective semantics; this preliminary study aimed at disentangling effects of prosody versus semantics.

Research to date suggests that while most language functions are left lateralized, the right hemisphere may have a preferential role in processing prosody (Ley and Bryden 1982). Stripped of lexical information, prosodic pitch changes and contours are processed by a right frontotemporal network (Tracy et al. 2011), or by right superior temporal gyrus (STG; Alba-Ferrara et al. 2012). This lateralization may reflect the right hemisphere's specialization for slower spectral cues, as prosody is signaled by acoustic cues that unfold over longer time scales (Poeppel 2003).

While many studies point to a right hemisphere network underlying affective prosody, others suggest a bilateral network. Bilateral superior temporal sulci (STS; Sander et al. 2005), inferior frontal gyrus (IFG; Hoekert et al. 2010), STG (Ethofer et al. 2012), and inferior frontal areas (Ethofer et al. 2006) all seem to respond to affective cues. Additional bilateral regions are implicated in processing of explicitly attended emotional prosody, including right middle temporal gyrus (MTG), right planum polare, left subgenual anterior cingulate cortex, left putamen, and left amygdala (Fruhholz et al. 2012). Thus, both cortical and subcortical regions participate in the proposed bilateral network. A bilateral network may underlie affective prosody, with low-level acoustic features of prosody drawing on right hemisphere components (Witteman et al. 2012). Wildgruber et al. (2009) proposed both bottom-up (extraction of signal properties) and top-down (emotional judgments involving memory system) routes for processing affective prosody in right hemisphere, with additional involvement of left inferior frontal gyrus (IFG).

Affective semantics has received less attention. Words with emotional connotations activate left anterior superior frontal gyrus (SFG), left anterior temporal cortex, left fusiform gyrus, left posterior cingulate gyrus, and left angular gyrus (Crosson et al. 2002). Left subgenual anterior cingulate cortex plays a role in processing emotionally pleasant and unpleasant words relative to neutral words (Maddock et al. 2003). Retrosplenial posterior cingulate gyrus is engaged in evaluating emotional salience (Cato et al. 2004). Hearing sentences with affective semantic content engages the left IFG, left posterior STS, and medial prefrontal areas (Beaucousin et al. 2007). Of note, findings are left-lateralized and rely on a general lexical-semantic network rather than emotion-processing regions (Binder et al. 2009).

Most prior research has either examined affective prosody or affective semantics, but not both. In studies that did target both these sources of affect, participants were explicitly instructed to attend to emotional cues (e.g. Vingerhoets et al. 2003). An examination of the neural response to emotion processing without explicit attention may reveal more ecologically valid neural substrates. Other studies that incorporated both prosody and semantics probed these channels separately (e.g. Ethofer et al. 2006). The present work employed a fully-crossed design that disentangles the relative contributions of these affective cues.

A preliminary functional magnetic resonance imaging (fMRI) study investigated the neural bases of processing angry sentences to characterize the distinct and overlapping neuroanatomical substrates of semantic versus prosodic cues to affect. We hypothesized the engagement of a bilateral frontotemporal network for prosody and a left lateralized temporoparietal network for semantics.

## Methods

Ten adults participated in an fMRI study. Two participants were excluded due to failed functional or structural scan acquisitions. Of the eight remaining participants, three were male and five were female. One participant was left-handed. All were native speakers of English. Participants ranged in age from 18 to 30 years with a mean age of 22.68 years ( $SD = 3.84$ ). All participants were college students. Participants consented to participation and were compensated for their time. All procedures were approved by the University of Connecticut Institutional Review Board.

Participants received training on the experimental task in a mock scanner. After training, participants were placed on the bed of the MRI scanner, and their heads were stabilized with foam cushions. They wore MRI-compatible earphones and viewed the experimental task through a mirror mounted on the head coil. In the scanner, participants heard a series of recorded declarative statements of three to five high-frequency words, spoken by a female native speaker of English. Statements expressed semantically neutral content or angry content, and were spoken with neutral or angry prosody. Words used in semantically angry and semantically neutral sentences were matched for frequency,  $t(268) = 0.30$ ,  $p = .76$ . Each sentence was scaled to an average intensity of 70 decibels. Across the four conditions, pitch range did not differ,  $F(3, 235) = 1.83$ ,  $p = .14$ . Across neutral and angry semantic conditions, each stimulus sentence was presented separately with neutral prosody and with angry prosody.

Prosodic and semantic valence (neutral, angry) were each confirmed via ratings from undergraduate participants. Using a scale from one to five, 11 raters judged the anger of sentences in text form; using the same scale, another group of 11 raters judged auditorally-presented sentences. Stimuli were included if their average ratings fell at the appropriate endpoints (either 1–2 or 4–5 on a five-point scale). Semantically neutral sentences included “This is a tall horse;” semantically angry sentences included “That game is not fair.” Participants reported via button press whether a sentence was about a living creature (50% were); this *implicit* engagement of affective semantics and prosody provided ecological validity. Four conditions resulted from crossing two levels of affective prosody (neutral, angry) with two levels of affective semantics (neutral, angry). Stimuli were presented pseudorandomly in an event-related design with six runs (316 s and 50 trials per run). Each run included ten trials in which an auditory control stimulus (beep) was presented. The auditory control condition is not discussed further as it was orthogonal to the research questions investigated here. The intertrial interval was jittered between four and twelve seconds.

MRI data were collected on a 3.0 Tesla Siemens Trio scanner at Yale University School of Medicine, with a 32-channel birdcage head coil. Six event-related functional runs were acquired in the axial anterior commissure–posterior commissure plane using a gradient echo, single-shot echoplanar sequence (TR = 2000, TE = 25 [2 subjects] or 20 [6 subjects], flip angle = 60° [2 subjects] or 80° [6 subjects], 32 slices,  $3.43 \times 3.43 \times 4$  mm voxels with no gap between slices). Differences in scanning parameters were accounted for in preprocessing, such that the group-level analysis was not impacted by individual-level scan acquisition differences. The first five images were discarded to account for T1 saturation effects. Three-dimensional MPRAGE anatomical images were acquired for coregistration and functional localization (176 slices,  $1 \text{ mm}^3$  isotropic voxels, TR = 2530, TE = 3.66, flip angle = 7°).

The fMRI data were analyzed in AFNI (Cox 1996). Preprocessing consisted of (a) slice-timing correction, (b) transformation from oblique to cardinal orientation, (c) motion correction using AFNI’s standard algorithm, (d) Talairach normalization via manual selec-

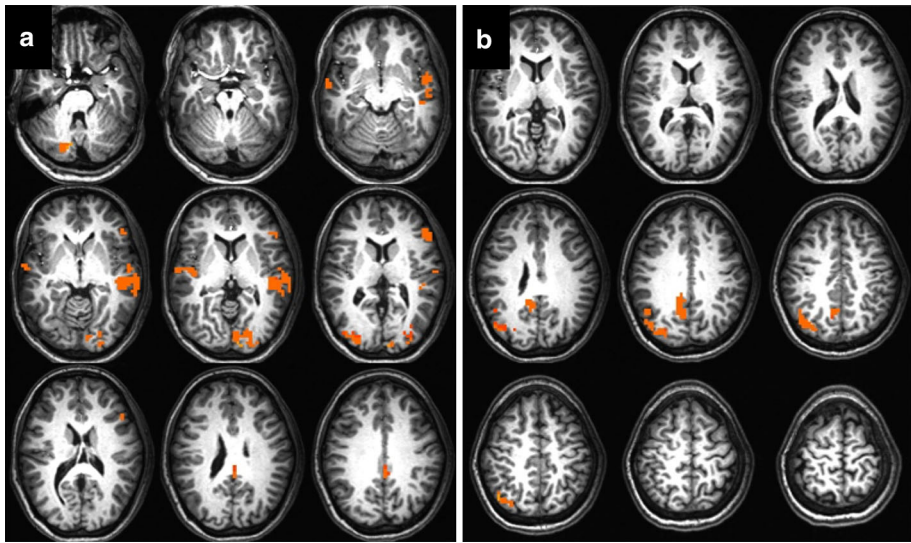
tion of anatomical landmarks, and (e) smoothing with a 6 mm Gaussian filter. Following preprocessing, each subject's raw voxel intensities were converted to percent signal change to standardize blood oxygen level dependent (BOLD) activation across space and time. The event time course was convolved with a gamma function (Cohen 1997) to generate a predictor time course by condition. For each subject, for each condition, we estimated the fit between the actual BOLD response time course at each voxel and the predicted hemodynamic response. Fit coefficients were entered into a repeated measures ANOVA. Prosodic emotion and semantic emotion *each* had two levels (neutral and angry). AlphaSim (AFNI) Monte Carlo simulations were implemented to estimate voxel-level alpha threshold and minimum cluster size, yielding cluster-level alpha thresholds to avoid false positive findings.

Main and simple effects were analyzed at the whole brain level for suprathreshold clusters of activation. Six contrasts were explored: (1) angry versus neutral prosody, (2) angry versus neutral semantics; (3) angry versus neutral prosody for angry and (4) neutral semantics; and (5) angry versus neutral semantics for angry and (6) neutral prosody. BOLD data were analyzed in two phases. First, we applied a voxel-level alpha threshold of  $p < .03$  and minimum cluster size of 53 voxels (cluster-level alpha of  $p < .05$ , corrected for multiple comparisons). Resulting activation clusters for the prosody contrasts were very large, spanning anatomical boundaries. To establish good anatomical separation of activation clusters—rather than accept unreasonable cluster sizes and questionable validity of results—a second analysis phase applied a stricter cluster-level alpha threshold of  $p < .001$  to evaluate each contrast. The combinations of voxel-level alpha threshold and minimum cluster size used to achieve this corrected, cluster-level alpha for each contrast were determined using a balanced approach in which anatomical separation of clusters was emphasized without being so strict as to purge clusters. For a given contrast, if activation clusters overlapped many distinct functional regions, the voxel-level alpha threshold was lowered until sufficient separation was achieved without eradicating the activation clusters altogether. In each case, the combination of voxel-level alpha and minimum cluster size used yielded a cluster-level alpha of  $p < .001$ , corrected for multiple comparisons according to AFNI's AlphaSim program. Results of the second phase of the analysis are presented with their voxel-level alpha thresholds.

## Results

Reaction time (RT) was shortest for neutral prosody/neutral semantics, followed by neutral prosody/angry semantics and angry prosody/neutral semantics, and then by angry prosody/angry semantics. A two-factor, within-subjects ANOVA for RT revealed an interaction of prosody and semantics,  $F(1, 6) = 9.20$ ,  $p = .02$ ,  $\eta_p^2 = .61$ . For semantically neutral sentences, RT to angry prosody was slower than RT to neutral prosody,  $t(6) = 8.95$ ,  $p = .0001$ . For semantically angry sentences, RT was slower for angry prosody,  $t(6) = 7.10$ ,  $p = .0004$ . For prosodically neutral sentences, RT to angry semantics was significantly slower than RT to neutral semantics,  $t(6) = 3.33$ ,  $p = .02$ . There was no difference between angry and neutral semantics for prosodically angry sentences,  $t(6) = 0.59$ ,  $p = .58$ .

The first-phase fMRI analysis identified local maxima within unwieldy clusters; these results are available upon request. Many of the first-phase results were robust to the stricter second-phase analysis. Results of the second-phase analysis showed elevated BOLD response to angry prosody compared to neutral prosody in eight regions: right IFG pars triangularis, right anterior STG/temporal pole, right STS/STG/middle temporal gyrus (MTG), left STG, left and right middle occipital gyri, right posterior cingulate gyrus, and left cerebel-



**Fig. 1** **a** Orange clusters indicate areas of greater BOLD activation for angry relative to neutral prosody.  $p < .001$ , cluster corrected. Serial horizontal slices are displayed from inferior ( $z = -18$ ) to superior ( $z = 30$ ). **b** Orange clusters indicate areas of greater BOLD activation for angry relative to neutral semantics.  $p < .001$ , cluster corrected. Serial horizontal slices are displayed from inferior ( $z = 26$ ) to superior ( $z = 44$ ). Images are oriented in neurological convention. Coordinates are in Talairach space (Color figure online)

lum (Fig. 1a). Examining the prosody contrast within angry semantics, the right precuneus showed elevated BOLD response for angry compared to neutral prosody. For neutral semantics sentences only, five regions showed elevated BOLD response for angry prosody: left IFG pars triangularis, right STS, right insula, right lingual gyrus, and right cerebellum/fusiform gyrus. Table 1 shows regions of activation.

Relative to neutral semantics, angry semantics elicited elevated responses in left angular gyrus and left precuneus/posterior cingulate gyrus (Fig. 1b). This effect reflected the sentences spoken with angry prosody, because the left precuneus/posterior cingulate gyrus cluster was also engaged in the simple effect contrast within angry prosody sentences only. For the subset of sentences spoken with neutral prosody, no significant areas of activation were observed. Table 1 shows regions of activation.

Thus, angry affect conveyed through both the prosodic and semantic channels yielded a substantially greater BOLD response than neutral affect. No suprathreshold elevated neural response was observed for neutral relative to angry stimuli; multiple regions showed increased activation for angry affect, including both classic language regions and other anatomical loci.

Because there was one left-handed participant, all contrast analyses were repeated without this participant's data. With a few exceptions<sup>1</sup>, results were nearly identical without the left-handed subject; contrasts yielding significant clusters of activation *with* the left-hander were the same contrasts that yielded significant clusters *excluding* the left-hander, and no newly

<sup>1</sup> For the contrast Angry > Neutral Prosody, the anterior STG/temporal pole cluster was not found. For the contrast Angry > Neutral Prosody for Neutral Semantics, the right lingual gyrus activation shifted to include the calcarine sulcus, and an additional cluster was found in right thalamus/caudate. For Angry > Neutral Semantics, the left precuneus/PCC cluster was not found, and left angular gyrus cluster expanded to include some occipital lobe.

**Table 1** Regions of BOLD activity for contrasts of interest

Side	Region	k	x	y	z	max	<i>t</i>
Angry prosody > neutral prosody (voxel-level $p < .001$ )							
R	STS/STG/MTG	123	62	-24	-2	.15	5.65
R	Middle occipital gyrus	71	7	-92	12	.18	5.51
L	STG	31	-62	-6	1	.15	5.58
R	IFG pars triangularis	28	48	28	1	.15	6.10
L	Middle occipital gyrus	21	-27	-89	15	.10	5.59
L	Cerebellum	16	-13	-71	-19	.16	6.66
R	Posterior cingulate gyrus	16	0	-37	32	.11	5.42
R	Anterior STG/temporal pole	15	54	-3	-2	.14	5.56
Angry prosody > neutral prosody for angry semantics (voxel-level $p < .005$ )							
R	Precuneus	39	3	-44	39	.12	4.05
Angry prosody > neutral prosody for neutral semantics (voxel-level $p < .0001$ )							
R	Cerebellum/fusiform gyrus	29	27	-41	-16	.18	7.98
R	Lingual gyrus	17	21	-79	1	.12	8.01
L	IFG pars triangularis	15	-41	17	5	.14	8.07
R	STS	14	45	-30	5	.17	10.30
R	Insula	13	38	-17	8	.15	7.99
Angry semantics > neutral semantics (voxel-level $p < .02$ )							
L	Angular gyrus	102	-31	-68	46	.10	3.74
L	Precuneus/posterior cingulate gyrus	60	-3	-48	25	.08	3.05
Angry semantics > neutral semantics for angry prosody (voxel-level $p < .035$ )							
L	Precuneus/posterior cingulate gyrus	118	-3	-54	46	.07	3.93

Voxel-level alpha values are presented. Cluster-level alpha values are all  $p < .001$ . *R* right, *L* left, *k* cluster size in voxels, *max* maximum beta value; coordinates are for maximum intensity voxel and are presented in Talairach space. Coordinates are presented in left, posterior, inferior (LPI) convention. *T* statistics are presented for peak voxels

significant clusters emerged after excluding the left-hander. Because activation patterns were similar with and without this participant, results are presented for all subjects.

## Discussion

In this study of affective language processing, we probed for differences in two linguistic streams of emotional information: prosody and semantics. We probed neural substrates of affect processing in language by contrasting angry prosody and semantics. Results demonstrate that processing of affective content, particularly affective prosody, implicates a wide network of neural regions spanning both hemispheres. One notable finding was the power of prosodic anger relative to semantic anger. Compared to semantic anger, prosodic anger (a) conferred a more substantial processing cost in reaction time, (b) yielded a more robust profile of BOLD activation, and (c) engaged more brain areas across both cerebral hemispheres.

The findings suggest that anger communicated through prosody is very different than anger communicated through semantics. The effects of angry prosody were powerful, whereas effects of angry semantics were subtle. This aligns with the intuitive sense that angry sounding



speech is unsettling, regardless of the content. Reaction times were slower for semantically angry sentences than semantically neutral sentences, but reaction times were even slower for sentences spoken with angry prosody, regardless of semantic valence. Slowed reaction times reflect a processing burden associated with the angry stimuli; perhaps the adaptive significance of the signal earns anger a more rigorous and time-consuming treatment by processing resources. Angry prosody is characterized acoustically by relatively high volume, high volume variance, low pitch, high pitch variance, fast rate, short duration, and few pauses (Sobin and Alpert 1999). This prosodic signature may serve as a more reliable set of cues than those conveyed in the semantic channel.

Neuroanatomical findings were consistent with prior results. Semantic anger processing was strongly lateralized to the left hemisphere; this confirmed work suggesting a primary role for left angular gyrus and left posterior cingulate cortex (Crosson et al. 2002). Prosodic anger engaged both hemispheres, as in previous research (e.g. Witteman et al. 2012). The observed involvement of *left* hemisphere regions in processing angry prosody supports a bilateral model as opposed to a strictly right lateralized model. In contrast to semantic processing, prosodic processing draws heavily on right hemisphere regions; however, findings do not support a strict right hemisphere argument for prosody.

While regions responding to angry prosody (bilateral temporal areas and bilateral IFG) have been observed in previous studies, other areas were implicated. Angry prosody engaged occipital areas (bilateral middle occipital gyrus and right lingual gyrus), right posterior cingulate gyrus, right insula, right precuneus, and bilateral cerebellum. Recruitment of occipital visual language areas in response to angry prosody may indicate that visualization is helpful for comprehending an emotionally important stimulus. Past studies have indicated a prominent role for the posterior cingulate gyrus in detecting emotional valence, particularly of autobiographical memories (Maddock et al. 2003). Emotional memory retrieval may be a contextual aspect of the neural response to angry prosody. The right insula is involved in processing emotional content and interoceptive awareness (Critchley et al. 2004). Emotional prosody could invoke autonomic bodily responses and cognitive evaluations of affective valence, for which the insula is ideally tuned. The precuneus is part of a network involved in self-representation (Lou et al. 2004). The integration of autobiographical episodic memories and emotional features of those memories may be summoned by affective cues from interlocutors. In sum, these areas may be components of a distributed affective prosody network.

While an activation peak in the left amygdala was identified in the first-phase analysis, we did not find activation for angry prosody in the amygdalae in the stricter second-phase analysis. Previous studies have highlighted the roles of both left and right amygdalae in processing of emotional prosody (Fruhholz et al. 2012; Sander et al. 2005), but our strictly-thresholded whole-brain analysis did not reflect involvement of subcortical emotional centers. This may reflect methodological constraints. The amygdalae comprise relatively few MRI voxels, at an average volume of less than two cubic centimeters each (Brabec et al. 2010). Because our second-phase analysis used a whole-brain approach, the thresholding may have masked amygdala involvement.

Methodological limitations suggest cautious interpretation. The fMRI study only included eight participants, though note that results were consistent between individuals. Even the inclusion of a left-handed participant did not alter the primary findings. Further, left-handed subjects are often excluded from fMRI studies of language because of more frequent right dominance for language; however, 73 % of strongly left-handed people have right hemisphere dominance for language (Knecht et al. 2000). Some have argued against systematic exclusion of left-handed participants, to capture the diversity of human brain function (Willems et al. 2014).

These results provide motivation for future work. One natural extension is to investigate other emotions besides anger using the same fMRI factorial design to permit more general conclusions about affective language processing. The question remains whether the neurofunctional networks elucidated in the current project serve all emotions or specifically anger. Future work should investigate neural substrates and personality features in the same participants. The prosodic information stream elicits a more substantial behavioral and neurobiological response, whereas the semantic information stream elicits a more subtle response. This suggests the nervous system may be more tuned to prosodic cues in speech.

**Acknowledgments** The authors gratefully acknowledge Haskins Laboratories and NSF 1144399 for funding, Deborah Fein for feedback, and Einar Mencl for assistance with programming the task.

#### Compliance with ethical standards

**Ethical standards** All procedures were in accordance with the ethical standards of the institutional review board and with the 1964 Helsinki declaration and its later amendments or comparable ethical standards. Informed consent was obtained from all individual participants included in the study.

**Conflict of interest** The authors declare that they have no conflict of interest.

## References

- Adolphs, R. (2002). Recognizing emotion from facial expressions: Psychological and neurological mechanisms. *Behavioral and Cognitive Neuroscience Reviews*, *1*(1), 21–62. doi:[10.1177/1534582302001001003](https://doi.org/10.1177/1534582302001001003).
- Alba-Ferrara, L., Ellison, A., & Mitchell, R. L. C. (2012). Decoding emotional prosody: Resolving differences in functional neuroanatomy from fMRI and lesion studies using TMS. *Brain Stimulation*, *5*, 347–353. doi:[10.1016/j.brs.2011.06.004](https://doi.org/10.1016/j.brs.2011.06.004).
- Beaucousin, V., Lacheret, A., Turbelin, M.-R., Morel, M., Mazoyer, B., & Tzourio-Mazoyer, N. (2007). fMRI study of emotional speech comprehension. *Cerebral Cortex*, *17*(2), 339–352. doi:[10.1093/cercor/bhj151](https://doi.org/10.1093/cercor/bhj151).
- Berckmoes, C., & Vingerhoets, G. (2004). Neural foundations of emotional speech processing. *Current Directions in Psychological Science*, *13*(5), 182–185. doi:[10.1111/j.0963-7214.2004.00303.x](https://doi.org/10.1111/j.0963-7214.2004.00303.x).
- Binder, J. R., Desai, R. H., Graves, W. W., & Conant, L. L. (2009). Where is the semantic system? A critical review and meta-analysis of 120 functional neuroimaging studies. *Cerebral Cortex*, *19*(12), 2767–2796. doi:[10.1093/cercor/bhp055](https://doi.org/10.1093/cercor/bhp055).
- Brabec, J., Rulseh, A., Hoyt, B., Vizek, M., Horinek, D., Hort, J., et al. (2010). Volumetry of the human amygdala—An anatomical study. *Psychiatry Research*, *182*(1), 67–72. doi:[10.1016/j.psychres.2009.11.005](https://doi.org/10.1016/j.psychres.2009.11.005).
- Cato, M. A., Crosson, B., Gökçay, D., Soltysik, D., Wierenga, C., Gopinath, K., et al. (2004). Processing words with emotional connotation: An fMRI study of time course and laterality in rostral frontal and retrosplenial cortices. *Journal of Cognitive Neuroscience*, *16*(2), 167–177.
- Cohen, M. S. (1997). Parametric analysis of fMRI data using linear systems methods. *NeuroImage*, *6*(2), 93–103. doi:[10.1006/nimg.1997.0278](https://doi.org/10.1006/nimg.1997.0278).
- Cox, R. W. (1996). AFNI: Software for analysis and visualization of functional magnetic resonance neuroimages. *Computers and Biomedical Research*, *29*(3), 162–173.
- Critchley, H. D., Wiens, S., Rotshtein, P., Ohman, A., & Dolan, R. J. (2004). Neural systems supporting interoceptive awareness. *Nature Neuroscience*, *7*(2), 189–195. doi:[10.1038/nn1176](https://doi.org/10.1038/nn1176).
- Crosson, B., Cato, M. A., Sadek, J. R., Gokcay, D., Bauer, R. M., Fischler, I. S., et al. (2002). Semantic monitoring of words with emotional connotation during fMRI: Contribution of anterior left frontal cortex. *Journal of the International Neuropsychological Society*, *8*, 607–622.
- Ekman, P. (1992). An argument for basic emotions. *Cognition and Emotion*, *6*(3/4), 169–200.
- Ethofer, T., Anders, S., Erb, M., Herbert, C., Wiethoff, S., Kissler, J., et al. (2006). Cerebral pathways in processing of affective prosody: A dynamic causal modeling study. *NeuroImage*, *30*(2), 580–587. doi:[10.1016/j.neuroimage.2005.09.059](https://doi.org/10.1016/j.neuroimage.2005.09.059).



- Ethofer, T., Bretschner, J., Gschwind, M., Kreifelts, B., Wildgruber, D., & Vuilleumier, P. (2012). Emotional voice areas: Anatomic location, functional properties, and structural connections revealed by combined fMRI/DTI. *Cerebral Cortex*, 22, 191–200. doi:10.1093/cercor/bhr113.
- Fruhholz, S., Ceravolo, L., & Grandjean, D. (2012). Specific brain networks during explicit and implicit decoding of emotional prosody. *Cerebral Cortex*, 22, 1107–1117. doi:10.1093/cercor/bhr184.
- Hoekert, M., Vingerhoets, G., & Aleman, A. (2010). Results of a pilot study on the involvement of bilateral inferior frontal gyri in emotional prosody perception: An rTMS study. *BMC Neuroscience*, 11, 93. doi:10.1186/1471-2202-11-93.
- Knecht, S., Dräger, B., Deppe, M., Bobe, L., Lohmann, H., Flöel, A., et al. (2000). Handedness and hemispheric language dominance in healthy humans. *Brain*, 123, 2512–2518.
- Ley, R. G., & Bryden, M. P. (1982). A dissociation of right and left hemispheric effects for recognizing emotional tone and verbal content. *Brain and Cognition*, 1, 3–9.
- Lou, H. C., Luber, B., Crupain, M., Keenan, J. P., Nowak, M., Kjaer, T. W., et al. (2004). Parietal cortex and representation of the mental Self. *Proceedings of the National Academy of Sciences of the United States of America*, 101(17), 6827–6832. doi:10.1073/pnas.0400049101.
- Maddock, R. J., Garrett, A. S., & Buonocore, M. H. (2003). Posterior cingulate cortex activation by emotional words: fMRI evidence from a valence decision task. *Human Brain Mapping*, 18(1), 30–41. doi:10.1002/hbm.10075.
- Poeppl, D. (2003). The analysis of speech in different temporal integration windows: Cerebral lateralization as “asymmetric sampling in time”. *Speech Communication*, 41(1), 245–255. doi:10.1016/S0167-6393(02)00107-3.
- Sander, D., Grandjean, D., Pourtois, G., Schwartz, S., Seghier, M. L., Scherer, K. R., et al. (2005). Emotion and attention interactions in social cognition: Brain regions involved in processing anger prosody. *NeuroImage*, 28(4), 848–858. doi:10.1016/j.neuroimage.2005.06.023.
- Sobin, C., & Alpert, M. (1999). Emotion in speech: The acoustic attributes of fear, anger, sadness, and joy. *Journal of Psycholinguistic Research*, 28(4), 347–365. doi:10.1023/A:1023237014909.
- Tracy, D. K., Ho, D. K., O’Daly, O., Michalopoulou, P., Lloyd, L. C., Dimond, E., et al. (2011). It’s not what you say but the way that you say it: An fMRI study of differential lexical and non-lexical prosodic pitch processing. *BMC Neuroscience*, 12, 128. doi:10.1186/1471-2202-12-128.
- Vingerhoets, G., Berckmoes, C., & Stroobant, N. (2003). Cerebral hemodynamics during discrimination of prosodic and semantic emotion in speech studied by transcranial Doppler ultrasonography. *Neuropsychology*, 17(1), 93–99. doi:10.1037/0894-4105.17.1.93.
- Wildgruber, D., Ethofer, T., Grandjean, D., & Kreifelts, B. (2009). A cerebral network model of speech prosody comprehension. *International Journal of Speech-Language Pathology*, 11(4), 277–281. doi:10.1080/17549500902943043.
- Willems, R. M., der Haegen, L. Van, Fisher, S. E., & Francks, C. (2014). On the other hand: Including left-handers in cognitive neuroscience and neurogenetics. *Nature Reviews Neuroscience*, 15(3), 193–201. doi:10.1038/nrn3679.
- Witteman, J., Van Heuven, V. J. P., & Schiller, N. O. (2012). Hearing feelings: A quantitative meta-analysis on the neuroimaging literature of emotional prosody perception. *Neuropsychologia*, 50, 2752–2763. doi:10.1016/j.neuropsychologia.2012.07.026.