



Research report

Auditory attention enhances processing of positive and negative words in inferior and superior prefrontal cortex



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ABSTRACT

Visually presented emotional words are processed preferentially and effects of emotional content are similar to those of explicit attention deployment in that both amplify visual processing. However, auditory processing of emotional words is less well characterized and interactions between emotional content and task-induced attention have not been fully understood. Here, we investigate auditory processing of emotional words, focussing on how auditory attention to positive and negative words impacts their cerebral processing.

A Functional magnetic resonance imaging (fMRI) study manipulating word valence and attention allocation was performed. Participants heard negative, positive and neutral words to which they either listened passively or attended by counting negative or positive words, respectively. Regardless of valence, active processing compared to passive listening increased activity in primary auditory cortex, left intraparietal sulcus, and right superior frontal gyrus (SFG). The attended valence elicited stronger activity in left inferior frontal gyrus (IFG) and left SFG, in line with these regions' role in semantic retrieval and evaluative processing. No evidence for valence-specific attentional modulation in auditory regions or distinct valence-specific regional activations (i.e., negative > positive or positive > negative) was obtained.

Thus, allocation of auditory attention to positive and negative words can substantially increase their processing in higher-order language and evaluative brain areas without modulating early stages of auditory processing. Inferior and superior frontal brain structures mediate interactions between emotional content, attention, and working memory when prosodically neutral speech is processed.

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1. Introduction

During spontaneous visual processing, when participants can allocate attentional resources freely to the stimuli presented, emotional stimuli are prioritized over neutral stimuli (e.g., Schupp, Junghöfer, Weike, & Hamm, 2003; Schupp et al., 2007). As the neural signature of this prioritized processing of emotional stimuli parallels effects of feature-based attention (Schupp, Flaisch, Stockburger, & Junghöfer, 2006), the preferential processing of emotional material is sometimes also referred to as “motivated attention” (Lang, Bradley, & Cuthbert, 1992). Selective processing of emotional stimuli is assumed to be biologically prepared, promoting survival via enhanced resource allocation and natural selective attention to intrinsically relevant stimuli (Bradley, Keil, & Lang, 2012).

However, the attention-grabbing properties of emotional stimuli also extend to emotionally arousing words whose emotional significance is ontogenetically learnt. Across several electrophysiology studies, preferential visual processing of emotionally arousing words (e.g., Herbert, Junghofer, & Kissler, 2008; Keuper et al., 2014; Kissler, Herbert, Peyk, & Junghofer, 2007; Kissler & Herbert, 2013; Trauer, Andersen, Kotz, & Müller, 2012; Trauer, Kotz, & Müller, 2015) has been found in similar time windows as during free viewing of emotional pictures (Junghöfer et al., 2001; Schupp et al., 2007), faces (Schupp et al., 2004), or gestures (Flaisch et al., 2015).

Functional magnetic resonance imaging (fMRI) studies likewise established enhanced haemodynamic activity for emotionally arousing compared to neutral words, both during passive processing (e.g., Herbert et al., 2009) and under specific task requirements such as lexical (Kuchinke et al., 2005; Nakic, Smith, Busis, Vythilingam, & Blair, 2006) or semantic decisions (e.g., Jackson & Crosson, 2006). During reading, emphasizing stimulus-driven processing, enhanced activation in extrastriate visual areas and limbic regions like the amygdala were found (Herbert et al., 2009). In contrast, during task-specific processing of emotion words such as semantic monitoring or lexical decisions, activations in prefrontal cortex and middle temporal gyrus (MTG), predominantly in the left hemisphere, have been reported (Cato et al., 2004; Jackson & Crosson, 2006; Kuchinke et al., 2005; Nakic et al., 2006).

Thus, for different, primarily visual stimuli, preferential processing of emotional content has been demonstrated, but a key question is how this bottom-up stimulus-driven processing of emotional material interacts with goal-driven top-down allocation of attention. In vision, the allocation of attention to stimulus features such as shape, colour or location in space has been shown to enhance activity in feature-specific extrastriate visual cortex regions (e.g., Corbetta, Miezin, Dobmeyer, Shulman, & Petersen, 1991, 1990; Schoenfeld, Hopf, Merkel, Heinze, & Hillyard, 2014). These effects are at least partly orchestrated by prefrontal brain structures (Corbetta & Shulman, 2002). EEG studies show that feature-based attention to emotional pictures (e.g., Ferrari, Codispoti, Cardinale, & Bradley, 2008; Schupp et al., 2007) as well as written words (Schindler & Kissler, 2016) amplifies their processing over visual cortex at distinct processing stages.

fMRI studies further demonstrated that attention to emotional faces increases activity in the right superior temporal sulcus (STS) (Narumoto, Okada, Sadato, Fukui, & Yonekura, 2001), which, as part of the core face processing system, is particularly involved in processing emotional facial expressions (Haxby, Hoffman, & Gobbini, 2000). This supports the notion that emotion and attention interact to amplify processing in stimulus-specific brain regions, although not all processing stages seem to be equally amplified by attention to emotion: For instance in Narumoto et al.'s (2001) study, fusiform areas exhibited face selectivity but no interactive effect of attention to emotion. Less research addressed auditory processing, but during passive listening auditory cortex has also been found to exhibit larger responses to emotional complex environmental sounds than to neutral ones (Plichta et al., 2011).

Spatial attention during dichotic listening amplifies contra-lateral auditory cortex responses (e.g., Jäncke, Buchanan, Lutz, & Shah, 2001). Auditory spatial attention to emotional (angry) prosody has been found to activate orbitofrontal and parietal brain regions. At the same time, attention-independent processing enhancement for angry prosody has been identified in regions of the auditory cortex such as the right middle STS as well as the right amygdala (Sander et al., 2005). Similarly, angry prosody has been found to evoke larger responses in right middle STS, irrespective of spatial attention (Grandjean et al., 2005) or whether the listener's task is focussed on semantic meaning or emotional prosody (Ethofer, Anders, Erb et al., 2006).

Overall, previous research into the relationship between emotion and attention suggests that emotional stimuli can be processed both along attention-dependent and attention-independent neural pathways whereby attention-dependent mechanisms appear to be orchestrated primarily via frontal cortical networks and operate on sensory processing.

However, so far, little is known about the functional neuroanatomy underlying auditory processing of emotional language content and its modulation by attentional demands. Extant studies mostly used EEG and focused on the visual modality: Electrophysiology studies showed preferential visual processing of emotional words to persist in spite of a distracting task (Kissler, Herbert, Winkler, & Junghofer, 2009), suggesting independent pathways. On the other hand, cuing attention to negative words facilitates processing at an early lexical (P2) and a late semantic integration (N400) processing stage (Kanske, Plitschka, & Kotz, 2011). Generally, attention to word content has been shown to reduce the semantic N400 component, indicating that pre-activation by attention facilitates semantic integration (Cristescu & Nobre, 2008). Recently, visual attention to word valence has been shown to result in parallel effects of emotion and attention on early ERPs, but interactive effects on late ERPs: the sources of these effects were localized in frontal and visual brain areas, with interactive effects localized in visual cortex (Schindler & Kissler, 2016). In the fMRI, visual cueing of attention to semantic word categories has been shown to activate language-related areas such as the left inferior frontal and left posterior temporal gyri (Cristescu, Devlin, & Nobre, 2006). So far, however, it is unclear how attention and emotional content interact in

auditory word processing and what brain regions are activated.

Furthermore, it remains to be determined, whether any effects can be differentiated according to sub-categories such as valence. Specific frontal cortex regions have been suggested to code for the hedonic value of emotional stimuli. Research into emotional responses to olfactory and gustatory stimuli showed that distinct left and right orbito-frontal areas code for unpleasant and pleasant valence, respectively (Anderson et al., 2003; Small et al., 2003). A study on emotional picture processing demonstrated the involvement of medial pre-frontal regions and the nucleus accumbens in processing picture valence (Sabatinelli, Bradley, Lang, Costa, & Versace, 2007). Regarding emotional words, one study using a self-reference judgement task identified posterior regions in right lateral orbito-frontal cortex and in the anterior insula as coding for increasing pleasantness, whereas more posterior regions of the right lateral orbito-frontal cortex were found to code for increasing unpleasantness (Lewis, Weekes, & Wang, 2007). By contrast, in a lexical decision task, Kuchinke et al. (2005) found activation in anterior and posterior cingulate gyrus as well as in hippocampus and lingual gyrus to differentiate between positive and negative words. A recent electrophysiology study localized rapid responses to the hedonic quality of words in the left middle temporal and inferior frontal regions for positive and the cingulate cortex for negative words (Keuper et al., 2013).

Ethofer, Anders, Wiethoff et al. (2006) contrasted haemodynamic activity elicited during valence ratings of acoustically presented words varying in affective content or prosody and found stronger left hemispheric activations when content valence was evaluated. These included the medial SFG, the left MTG and left orbito-frontal structures, including IFG. It is unclear, however, whether any of these regions differentiated further between positive and negative valence.

Against the above background, the present study investigates the brain regions involved in the processing of emotional words during passive listening and active attention deployment to emotional word valence (positive or negative), aiming to delineate main effects of attention and emotion in auditory word processing and in particular their interaction.

We studied to what extent directing attention to the emotional valence of the words would activate regions involved in perceptual auditory processing, or temporal and prefrontal brain regions involved in semantic processing. Finally, we investigated regional differences between positive and negative word valence.

Participants were asked to listen to negative, positive or neutral words, while different instructions were given. Firstly, a passive listening run was used to test for brain regions showing increased activation for emotional compared to neutral words during spontaneous processing. Secondly, two runs were presented where attention had to be allocated either to positively or to negatively valenced words, thereby introducing a modulation of top-down attentional word selection, enabling the analysis of effects of attention on emotional word processing and valence-specific effects.

Two complementary analysis strategies were chosen: On the one hand, a whole-brain analysis was used to uncover experiment-induced activations in a data-driven manner. On

the other hand, haemodynamic activity was assessed in three a priori chosen regions of interest (ROI) representing low-level perceptual and high-level semantic areas whose involvement in sensory and semantic language processing is frequently suggested in the literature to specifically examine the processing level at which any attention-dependent modulations might occur.

2. Methods

2.1. Participants

Seventeen right-handed students volunteered to participate in the study, receiving 15 Euros as compensation. All participants were native speakers of German. They all met inclusion criteria for magnetic resonance imaging studies as assessed by a written questionnaire and all provided written informed consent to participate in the study. Upon interview, participants reported no history of neurological or psychiatric illness or any hearing problems. Two data sets had to be discarded due to technical difficulties, leaving data of fifteen participants (9 women, mean age: 24 years, range: 19–30 years) for subsequent analyses.

2.2. Stimuli

54 German adjectives served as stimuli, consisting of 18 highly arousing negative, 18 highly arousing positive, and 18 neutral words that had been previously assessed using the nine-step Self-Assessment Manikin's valence and arousal scales (SAM; Bradley & Lang, 1994). Stimuli were presented as audio files, taken from a larger database (Ethofer, Anders, Erb et al., 2006; Ethofer, Anders, Wiethoff et al., 2006). For all valence categories, words were spoken with neutral prosody. Prosody of words spoken by either male or female actors (actors' gender balanced within each category) had been evaluated in a pre-study including 42 participants (21 women, mean age: 29 years). Across valence categories, adjectives were matched for word length, word frequency, stimulus pitch and intensity as well as duration. On average, uniqueness points as extracted from the CELEX database (www.celex.mpi.nl) did not differ between the word categories (mean, median, and modal uniqueness points respectively were: pos-neg: 2.83, 2.5, 2; neg-ntr: 2.5, 2, 2; pos-ntr: 2.44, 2, 2; all comparisons were $p > .3$ on both parametric and non-parametric tests). Properties of the selected adjectives are summarised in Table 1. Supplementary Table 1 lists all words used in the German original, together with an English translation.

2.3. Design and procedure

In an event-related fMRI study, stimuli were presented acoustically via MRI-compatible headphones, sufficiently shielded from scanner noise to ensure clear perceptibility (Mr confon GmbH, Magdeburg, Germany; www.mr-confon.de). Similar to our previous studies in the visual (Herbert et al., 2009) and auditory (Ethofer, Anders, Erb et al., 2006; Ethofer, Anders, Wiethoff et al., 2006) domains, a slow event-related fMRI design was employed with a mean inter stimulus

Table 1 – Characteristic of word stimuli used. See Supplementary Table 1 for the full list of words (original and translation).

Variable	Word Category						Inferential statistics
	Negative		Positive		Neutral		
	M	SD	M	SD	M	SD	
Valence	3.07	.51	7.01	.48	5.15	.54	$F(2,51) = 267.01, p < .001, \eta^2 = .91$
Arousal	5.48	.90	5.58	.95	3.22	.41	$F(2,51) = 50.79, p < .001, \eta^2 = .67$
Word length	8.56	2.01	9.82	3.09	8.61	3.29	$F(2,51) = 1.39, p = .259, \eta^2 = .05$
Word frequency	951.83	2221.92	868.29	2598.64	1661.39	2177.60	$F(2,51) = .62, p = .543, \eta^2 = .02$
Pitch (Hz)	154.28	48.75	161.73	41.51	151.33	41.57	$F(2,51) = .27, p = .767, \eta^2 = .01$
Intensity (dB)	77.01	2.61	76.74	2.26	76.47	3.50	$F(2,51) = .16, p = .849, \eta^2 = .01$
Sound duration (ms)	802	189	745	231	731	110	$F(2,51) = .75, p = .47, \eta^2 = .03$

Valence ratings ranged from 1 (very unpleasant) to 9 (very pleasant). Arousal ratings also ranged from 1 (very low arousal) to 9 (very high arousal). Word frequency based on counts for written German from the DLEX database (<http://dlexdb.de/>).

interval of 12 sec (± 1.5 sec jitter). The experiment consisted of three runs, each run starting with a different instruction. All 54 adjectives were used in each of the three runs, which differed only in word order and attention instructions.

The experiment always started with a passive listening run, where participants' attention was still unbiased (see also Kissler et al., 2009; Schindler & Kissler, 2016). In the subsequent two runs, participants were instructed to pay attention to either negative or positive words by silently counting each adjective belonging to the target category, with the order of active runs balanced across participants. After each run, participants were asked to report the number of words they had counted. At the end of the experiment, outside the scanner, in a surprise memory test participants were asked to write down as many of the presented words as they could remember to assess their task involvement and any mnemonic effects of the experiment. Post-experimental individual stimulus appraisals were also obtained using nine-point valence and arousal ratings (see Table 1). The experiment was generated using Presentation software (www.neurobs.com).

2.4. Acquisition protocol

MRI data were collected using a 1.5T PHILIPS Inera Scanner equipped with an 8-channel SENSE head coil and power gradients. A high-resolution T1TfE structural scan was acquired with 200 sagittal slices (slice thickness = 1 mm, in-plane resolution = 1×1 mm). T2*-weighted functional echo-planar images (EPI) were acquired with 36 axial slices (TR = 3000 msec, TE = 40 msec, Flip Angle = 90° , Field of View = 240×240 mm, slice thickness = 3.5 mm, in-plane resolution = 3×3 mm). 221 volumes were acquired for each of the three runs, each run lasting approximately 11 min.

2.5. Preprocessing of fMRI data

Preprocessing was performed using SPM8 (www.fil.ion.ucl.ac.uk/spm/). Time series were corrected for head motion, field distortions and interactions between motion and distortions (Anderson et al., NeuroImage 2001). Motion associated with noticeable signal intensity changes was identified and corrected using the ArtRepair Toolbox (Mazaika, Whitfield, & Cooper, 2005). In the overall sample .5% of volumes were

interpolated (maximum of 2.1% in a single participant). For co-registration of functional and structural volumes, T1 images were brain extracted using the BET algorithm (Smith, 2002) and co-registered to the mean functional image. Normalisation of functional images was performed by using deformation fields derived from the normalisation of structural images obtained during segmentation of the T1 images (Ashburner & Friston, 2005). The derived forward deformation fields were applied to the realigned functional images (resampled voxel size = $2 \times 2 \times 2$ mm) and smoothed with a Gaussian kernel of 8 mm (full width at half maximum).

2.6. Analysis of fMRI data

Statistical analysis of data was performed using SPM8 (www.fil.ion.ucl.ac.uk/spm/), Marsbar (<http://marsbar.sourceforge.net/>; Brett, Anton, Valabregue, & Poline, 2002), the WFU Pick-Atlas (<http://fmri.wfubmc.edu/software/PickAtlas>) and SPSS20. On the single-subject level, each of the nine conditions (3 runs, 3 word types) was modelled with the haemodynamic response function (HRF) and its time derivative. Events were modelled as delta functions with zero duration (see also http://www.fil.ion.ucl.ac.uk/spm/course/slides11/08_Event_Related_FIL2011May.pdf). The contrast image for the comparison of each HRF regressor against baseline (no auditory stimuli) was then taken to the group level, where a full-factorial 2nd level analysis with the factors “run type” and “word type” was used. Percent signal change as an effect size estimate and finite impulse response time-courses were additionally computed using Marsbar and analysed using SPSS.

An unconstrained non-directional 3×3 ANOVA whole-brain analysis was performed with the factors run (passive, attend negative, attend positive) and word type (negative, positive, neutral), to investigate the overall presence of main and interaction effects, yielding the design shown in Table 2.

All significant clusters of the whole-brain analyses were also entered into the NeuroSynth database, to derive information on the cognitive processes typically associated with these activations (cf. Poldrack, 2006).

ROI analysis for beta values extracted from predefined regions (IFG, MTG, STG) for each run and condition was additionally performed in SPSS.

Table 2 – Set-up of the whole-brain 3×3 ANOVA (the 9 theoretically possible differential effects of word type dependent on run can be reduced to the currently illustrated 4-contrast solution, cf. <http://www.fil.ion.ucl.ac.uk/~wpenny/publications/spm-book/anova.pdf>).

Passive listening			Attention to negative			Attention to positive		
Negative	Positive	Neutral	Negative	Positive	Neutral	Negative	Positive	Neutral
0	0	0	1	-1	0	-1	1	0
0	0	0	0	1	-1	0	-1	1
-1	1	0	0	0	0	1	-1	0
0	-1	1	0	0	0	0	1	-1

2.7. ROI

Based on theoretical considerations about different stages of auditory word processing, a priori defined ROIs with high specificity for word processing were selected using the NeuroSynth meta-analytical database (Yarkoni, Poldrack, Nichols, Van Essen, & Wager, 2011; <http://old.NeuroSynth.org>). Reverse inference maps were used, as they reflect the probability of a study containing a certain term, given activity in that voxel, and thus allow estimating specificity of the region for the given keyword. The database was queried for the terms “speech”, “words”, and “language”, as these were represented by a reasonably large number of studies in the database and the regions involved represent different levels of auditory word processing (cf. Table 3). The peak voxel was derived from every map and the top 500 voxels belonging to the cluster of that peak voxel were extracted, with the resulting ROI size (4 cm^3) being roughly equivalent to a 10 mm sphere. Since the ROIs are based on aggregated previous functional data and not solely on anatomy, this should reduce the danger of averaging over functionally heterogeneous areas (cf. Friston, Rotshtein, Geng, Sterzer, & Henson, 2006). The three extracted left-

hemisphere ROIs correspond anatomically to IFG, proximal to Broca's Area (“words”), middle temporal gyrus (MTG; “language”) and STG, overlapping with Heschl's Gyrus (“speech”). Compare Fig. 1 and Table 2 for additional information on the extracted ROIs.

3. Results

3.1. Behavioural data

Participants counted on average 19.33 (SD 4.82) positive and 17.47 (SD 4.63) negative words, with counting performance not differing between conditions ($F(1,14) = 1.30, p = .27$). After the experiment, they remembered on average 6.53 (SD = 2.82) positive words, 5.53 (SD = 2.69) negative words, and 4.60 (SD = 2.29) neutral words, reflecting a memory advantage for emotional words ($F(2, 28) = 4.12, p = .03$). Specifically, positive words were recalled significantly better than neutral ones ($t(14) = 2.36, p = .03$), negative words were recalled somewhat better than neutral ones ($t(14) = 1.79, p = .1$) and recall of positive and negative words did not differ ($t(14) = 1.54, p = .14$).

Table 3 – Keywords used for ROI definition in the NeuroSynth search query.

Keyword	#Studies	Peak voxel			Side	Anatomical label
Words	698	-49	22	18	L	Inferior frontal gyrus
Language	413	-53	-40	0	L	Middle temporal gyrus
Speech	290	-59	-14	4	L	Superior temporal gyrus

Reverse inference maps, $p(\text{word}|\text{activation})$, were used to derive the top 500 voxel around each global maximum; peak voxel with highest posterior probability score labelled with x y z. Anatomical labelling according to LONI brain atlas (Shattuck et al., 2008).

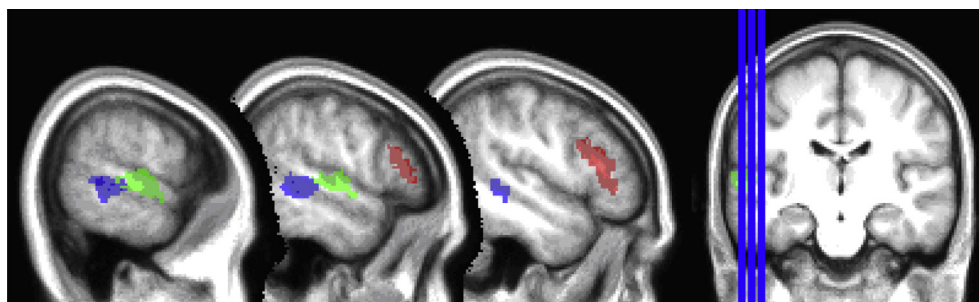


Fig. 1 – A priori defined regions of interest. Regions of interest (ROIs) as extracted using NeuroSynth; red – “words”; green – “speech”; blue – “language” ROI; sagittal slices shown correspond to $x = -60, x = -54, x = -48$ in MNI space, respectively; left of image is left of brain for coronal view; figure created using Mricron (<http://www.mccauslandcenter.sc.edu/mricron/mricron/>).

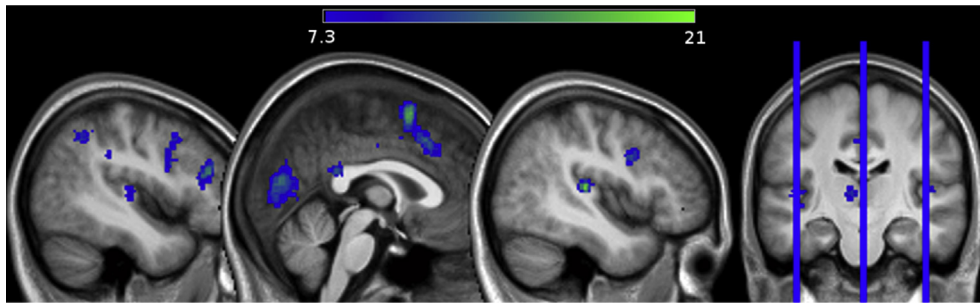


Fig. 2 – Whole-brain results of the main effect of run. Blue-green colour scale shows results thresholded at $p < .001$ uncorrected with a $p < .05$ cluster-level FWE correction; colour-coding as scaled in the upper-hand bar reflects size of F-Values.

Table 4 – Results for main effect of run: Active runs induced more BOLD response than did the passive run. Significant peak voxel for the main effect at $p < .05$ FWE-corrected; Anatomical labels chosen according to LONI Atlas (LPBA40); NeuroSynth labels report top three terms for the probability of activity in that voxel given the keyword (F: forward inference), and the probability of the presence of a keyword given activity in that voxel (R: reverse inference).

Region	Side	Volume mm ³	MNI coordinates			Z	Top Neurosynth labels
			X	Y	Z		
Superior temporal gyrus (STG)	R	40	44	−26	10	5.3	F: auditory, auditory cortex, heschl R: Heschl, primary auditory, pitch
Superior frontal gyrus (SFG)	R	24	2	10	60	5.1	F: sma, supplementary, supplementary motor R: pre sma, pre supplementary, sma
	R	16	8	16	44	5.0	F: task, conflict, working R: distractors, task difficulty, attentional control
Superior parietal lobule (SPL)	L	8	−30	−52	42	5.0	F: intraparietal, intraparietal sulcus, working memory R: shifting, orthographic, intraparietal

Table 5 – Post-hoc analyses of the main effect of run regardless of content. Pairwise repeated-measures t-tests ($df = 14$) for the significant clusters of the main analysis.

Region	Attend negative versus passive		Attend positive versus passive		Attend positive versus attend negative	
	t	p	t	p	t	p
STG (44 −26 10)	6.08	<.001	3.71	.002	−2.15	.049
SFG (2 10 60 and 8 16 44)	6.00	<.001	6.74	<.001	.34	.739
SPL (−30 −52 42)	6.57	<.001	4.64	<.001	−1.90	.079

3.2. Whole-brain analysis

There was a main effect of run (i.e., allocation of attention; results of F-Test shown in Fig. 2), which was explained by the attention to negative and attention to positive words both leading to significantly stronger regional activations than did the passive run (all $p < .001$), while the two attended runs did not differ from each other. This pattern emerged both when the peak cluster of the whole brain analysis (in auditory cortex, .05 FWE-corrected) was used to extract activations as well as when the activation was extracted and averaged from all clusters significant at $p < .001$ uncorrected. No main effect of emotion was found. Brain structures with main effects for the factor “run” are detailed in Table 4. Table 5 shows the results of the respective post-hoc analyses.

For the interaction effect of attention instruction and word type, significant clusters (FWE-corrected; $p < .05$) in the IFG and SFG were identified (Fig. 3, Table 6), indicating these regions to be involved in mediating emotion–attention interactions during word processing. To provide a heuristic regarding the likely functional role of the activated brain regions on the basis of typical association patterns in previous studies, the peak coordinates of main and interaction effects were entered into the NeuroSynth database and the top labels for the respective coordinates are reported (see Tables 4 and 6). More extensive discussion of these areas’ functional significance is provided in the discussion section on the basis of specific previous studies from the literature.

Results of whole-brain post-hoc analysis of the main effect of run, comparing attended stimuli versus unattended stimuli are provided in Table 5:

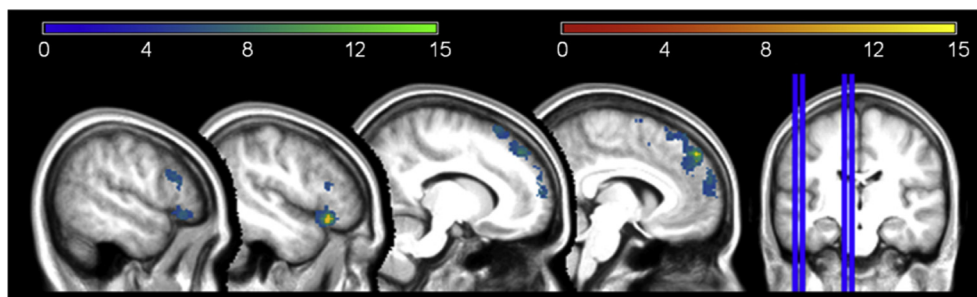


Fig. 3 – Whole-brain results of the 3×3 ANOVA emotion \times attention interaction effect: Blue-green colour scale shows results thresholded at $p < .001$ uncorrected with a $p < .05$ cluster-level FWE correction; red-yellow colour scale shows results thresholded at $p < .05$, FWE-corrected; colour-coding as scaled in the upper bars reflects size of F -Values.

Table 6 – Results for interaction run \times word content. Significant peak voxel for the interaction effect at $p < .05$. FWE-corrected; Anatomical labels chosen according to LONI Atlas (LPBA40); NeuroSynth labels report top three terms for the probability of activity in that voxel given the keyword (F: forward inference), and the probability of the presence of a keyword given activity in that voxel (R: reverse inference); keywords retrieved on 4 Jul 2016.

Region	Side	Volume mm ³	MNI coordinates			Z	Top Neurosynth labels
			X	Y	Z		
Inferior frontal gyrus	L	136	-46	26	-12	5.5	F: comprehension, semantic, sentences R: language comprehension, language network, tom
Superior frontal gyrus	L	96	-6	50	42	5.9	F: mpfc medial prefrontal, beliefs R: beliefs, negative neutral, remembering
	L	8	-6	50	36	5.0	F: self, social, self-referential R: self-referential, referential, medial superior

3.3. Post-hoc analyses for the emotion by task interaction effect

To determine the underlying pattern and direction of interaction effects between run and word type in the identified areas, percent signal change scores were extracted from each region and post-hoc compared between conditions (Fig. 4, Table 8).

Furthermore, to visualize the pair-wise comparisons underlying the interaction, the brain activation pattern comparing cerebral responses elicited by negative and positive words during the attend to positive and attend to negative runs are shown as t-maps in Fig. 5. The calculation of these t-map comparisons is based on the contrasts specified in Table 7.

In the passive run, only the negative word > positive word comparison became significant in IFG (Fig. 4). Regional activity elicited in the active runs by the attended versus unattended words is shown in Fig. 5. In these runs with attention instructions, post-hoc tests revealed attention-congruent effects in both IFG and SFG, with negative words in the negative attention run and positive words in the positive attention run yielding stronger activity than in the respective incongruent condition (Figs. 4 and 5; Table 8). Therefore, the previously identified interaction effects can be explained by increased activity for the currently attended emotion category. Moreover, neutral words were also affected by the attention instruction showing a response pattern similar to that of the

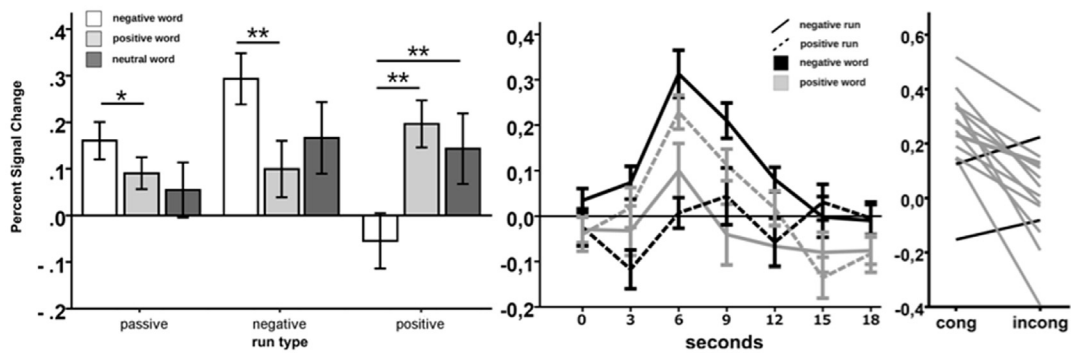
attended category, in particularly when positive words were the target (Fig. 4, Table 8).

3.4. ROI analysis

To specifically focus the analysis on a priori defined perceptual and higher-order language areas, whose activity could theoretically be expected to vary with task and word type, and in order to determine the relative involvement of sensory or semantic areas in the current experiment, a ROI analysis was conducted on three ROIs extracted from the NeuroSynth database (IFG (including Broca's area), MTG and superior temporal gyrus (STG)).

Results of the respective 3 (run) \times 3 (word type) ANOVAs for each region are displayed in Fig. 6. Interactions between task and content were confirmed in IFG ($F(4, 56) = 10.42, p < .001, \eta^2 = .43$) and in MTG ($F(4, 56) = 3.53, p = .027, \eta^2 = .20$), but no interaction was found in STG even with this targeted analysis ($F(4, 56) = 1.73, p = .156, \eta^2 = .11$). Post-hoc pair-wise comparisons show that for the IFG, attention-congruent effects are explained by negative words in the negative attention run and positive words in the positive attention run yielding stronger activity than in the respective incongruent condition (Fig. 6, Table 9). The IFG ROI also showed a significant negative > positive and negative > neutral effect specifically during silent listening, while in MTG a clearly significant attention-congruent effect was only present for the run with attention to positive words. No such attention-congruent

Inferior Frontal Gyrus (cluster at -46 26 -12)



Superior Frontal Gyrus (clusters at -6 50 42 and -6 50 36)

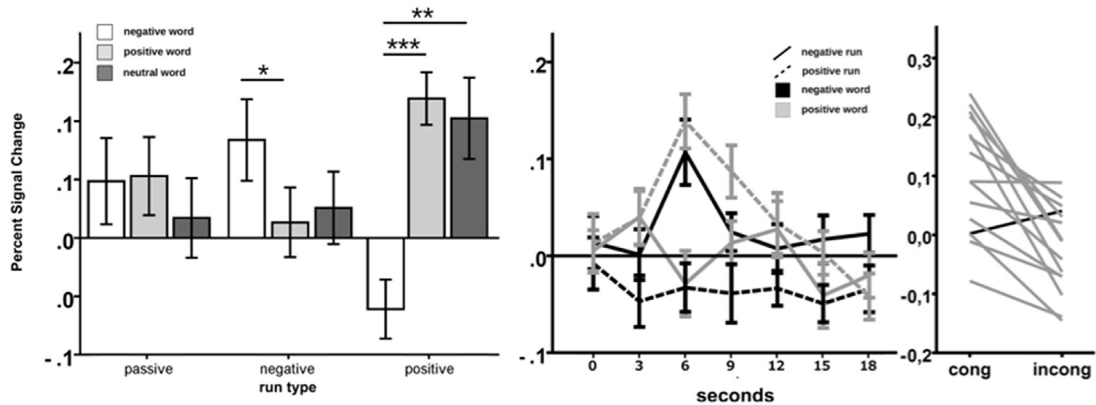


Fig. 4 – Percent signal change estimates for the whole-brain identified cluster. Percent signal change was extracted for each participant; left hand of figure shows percent signal change values for each of the nine regressors, significant differences within each run are denoted with: * $p < .05$, ** $p < .01$, *** $p < .001$; error bars denote standard error of the mean; middle row of figure shows time courses for negative and neutral words in both attention runs; right hand of figure shows single-participant values for attention-congruent and attention-incongruent conditions; cong, averaged congruent conditions; incong, averaged incongruent conditions.

Table 7 – Contrasts for the pair-wise comparisons shown in Fig. 5.

Passive listening			Attention to negative			Attention to positive		
Negative	Positive	Neutral	Negative	Positive	Neutral	Negative	Positive	Neutral
0	0	0	0	0	0	-1	1	0
0	0	0	1	-1	0	0	0	0

Table 8 – Post-hoc analyses. Pairwise repeated-measures t-tests ($df = 14$) for the significant clusters of the interaction analysis; SFG, superior frontal gyrus; IFG, inferior frontal gyrus; “passive”, passive listening run, “negative” run with attention to negative words, “positive”, run with attention to positive words; “ntr versus neg“ comparison of neutral and negative words; “ntr versus pos“, comparison of neutral and positive words; “neg versus pos” comparison of negative and positive words.

Region	Run type	neg versus ntr		pos versus ntr		neg versus pos	
		t	p	t	p	t	p
IFG	Passive	1.95	.071	.72	.483	2.45	.028
	Attend negative	2.12	.053	-1.24	.235	4.14	.001
	Attend positive	-3.71	.002	.73	.479	-4.00	.001
SFG	Passive	1.30	.214	1.11	.285	-.11	.912
	Attend negative	1.46	.165	-.39	.704	2.39	.031
	Attend positive	-4.10	.001	.53	.601	-6.16	<.001

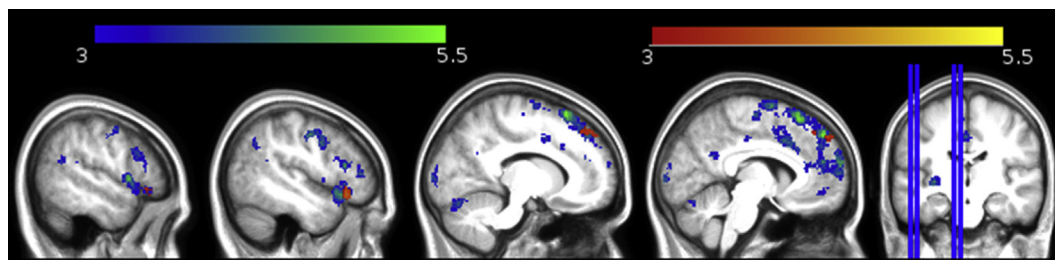


Fig. 5 – Blue-Green: T-values for “run: attention to positive stimuli; positive stimuli > negative stimuli”. Red-Yellow: T-values for “run: attention to negative stimuli; negative stimuli > positive stimuli”. $T = 3.16$ is $p < .001$ uncorrected. Results are presented with a cluster threshold of $p < .05$ (FWE-corrected).

effect was found in STG, which instead showed a small preference for positive content in the active runs (Table 9). In the active runs, processing of neutral words was also increased by attention, as reflected by significantly higher activity compared with the unattended category. Overall, clear interaction effects with higher activity for the attended run were only present for the IFG ROI, while in MTG an attention-congruent effect was only present for the run with attention to positive words. For auditory sensory regions no overall significant effects were found.

A comparison of the magnitude of valence-congruent attention modulation effects across ROIs, confirmed largest signal change in IFG, both in comparison to MTG and STG (Fig. 7). MTG, in turn, exhibited stronger task effects than STG. Effects in the IFG ROI were also in line with IFG-results of the whole-brain interaction analysis, the ROI showing considerable with the IFG results obtained in the whole brain analysis (see Supplementary Fig. 1).

4. Discussion

This study investigated how auditory word processing is modulated by top-down allocation of attention to positive or negative word valence. Mass-univariate whole-brain analysis identified main effects of run, regardless of the direction of instruction (positive or negative), in right STG and SFG, as well as left intraparietal brain structures. In line with increased recruitment of fronto-parietal attention networks and auditory brain structures, all of these regions increased their activity when participants were actively engaged with the task. These activations for the main effect of attention are in line with previous results from dichotic listening tasks (Jäncke et al., 2001; Sander et al., 2005). Although STG activity was strongest in the attention to negative run, no valence-congruent pattern was found in the aforementioned regions. By contrast, congruent effects of valence-specific attention allocation were found in left IFG and SFG.

In agreement with the whole-brain analysis, analysis of a priori defined ROIs confirmed the IFG ROI as exhibiting a valence-congruent response pattern. During passive listening, emotion effects were generally small and only the IFG ROI showed increased activation for negative words. ROI analysis of STG, specifically targeting perceptual processing modulation by emotional language content, revealed somewhat

increased activation for positive content in the active processing runs, but this did not converge with the whole brain analysis. Crucially, neither STG nor MTG showed valence-congruent modulation during the task.

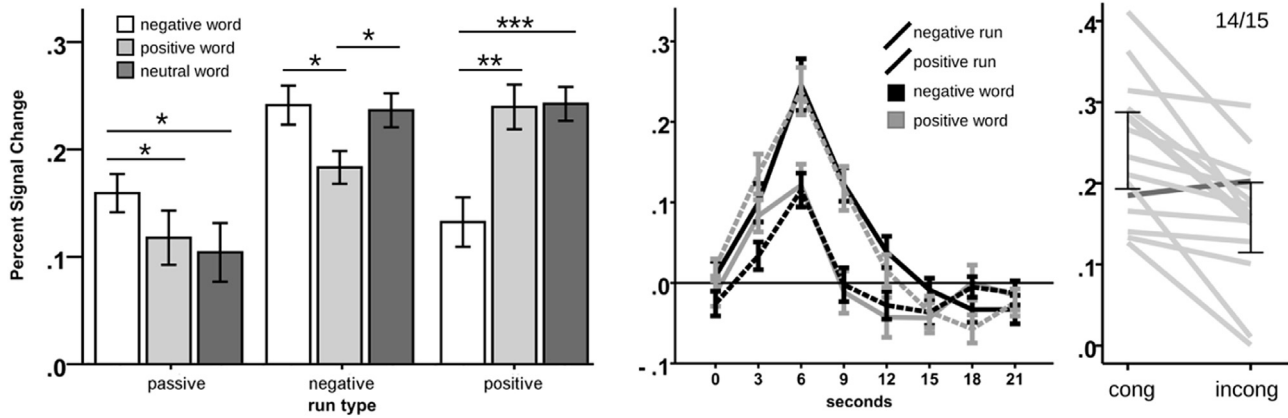
Overall, interaction effects were most robust in IFG, where whole-brain and ROI results overlapped almost perfectly (see Supplementary Fig. 1). Direct statistical comparisons of activity magnitude in a-priori defined brain regions showed that the valence-congruent modulation was significantly larger in IFG than in MTG and STG, indicating a more important role of brain regions higher in the processing hierarchy for mediating attention–valence interactions in auditory language processing when prosody is neutral.

Although not associated with an explicit instruction, neutral words were also modulated by attention. First, for all words, regardless of their valence, recruitment of auditory structures increased in both active runs, the largest increase occurring during the “attention to negative” run. Second, in the higher-order language areas, neutral words tended to pattern with the target category, which may be due to ambiguities of this word class, as some authors argue that neutral valence is not a valid natural kind (see e.g., Scherer, 2013) or due to participants’ evaluation strategies. Selection on the basis of “non-target exclusion” might be one such strategy.

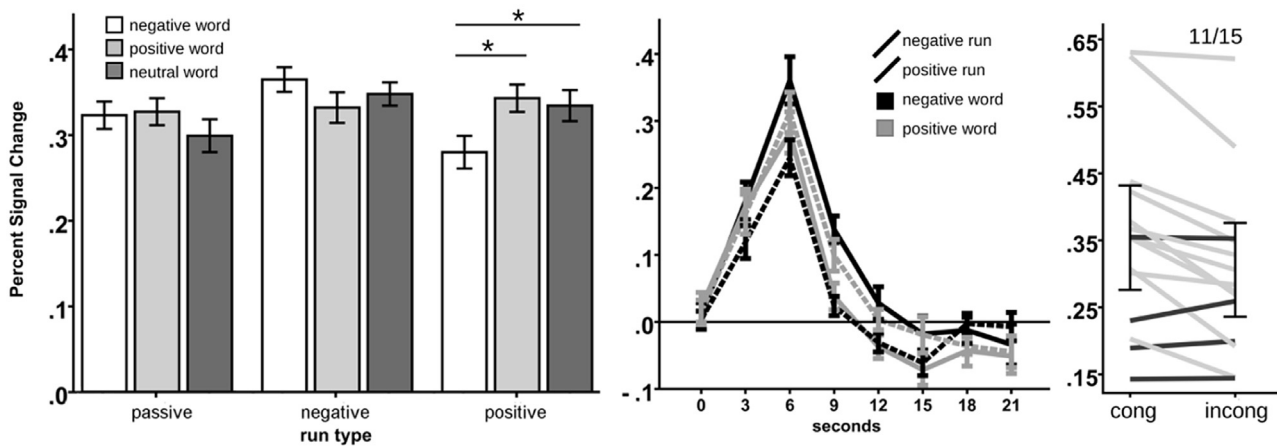
Overall, present results indicate that for auditory word processing, higher order language-related brain areas may mediate the interaction of emotional content and task requirements in a similar manner, as previously shown for other types of semantic processing (e.g., Roskies, Fiez, Balota, Raichle, & Petersen, 2001). Left IFG has also been found to mediate the interaction between emotional word content and prosody, particularly in females (Schirmer, Zysset, Kotz, & von Cramon, 2004).

Lower-level perceptual processing (STG) responded with an unspecific BOLD increase in the active runs. Because the passive listening run was always first, order-effects could have contributed to this pattern. However, as in previous studies (Kissler et al., 2009; Schindler & Kissler, 2016), we reasoned that emotion-specific carry-over effects from passive to active runs should be smaller than vice versa. Stimulus repetition across the three runs could have resulted in habituation of the BOLD response. Empirically, the data show no evidence of habituation and, if present, the active processing instruction during the last two runs apparently effectively counteracted it. Repetition suppression (habituation) has been

Inferior frontal gyrus (words)



Medial temporal gyrus (language)



Superior temporal gyrus (speech)

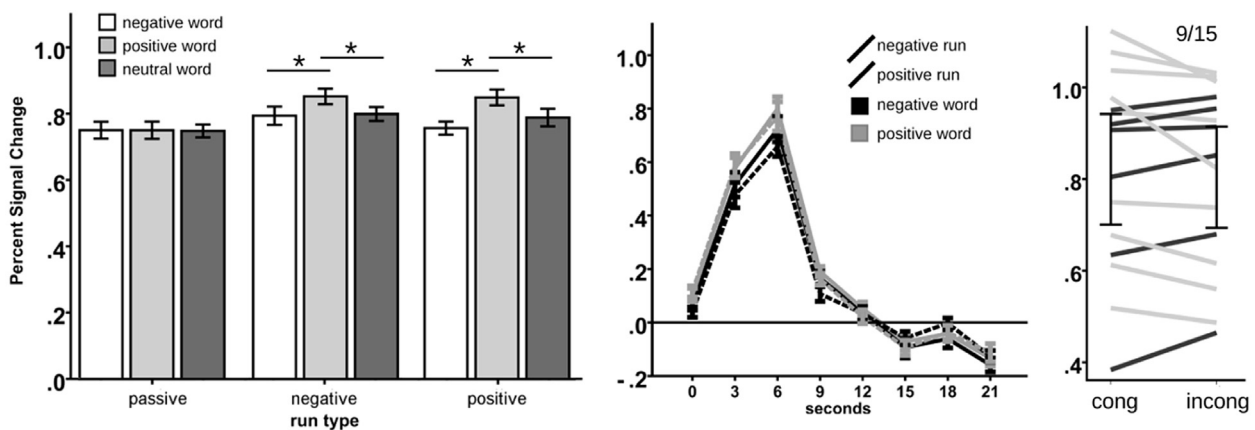


Fig. 6 – PSC Results for a prior defined ROIs. Le Left hand of figure shows percent signal change values for each of the nine regressors, significant differences within each run are denoted with * $p < .05$, ** $p < .01$ and *** $p < .001$; error bars denote standard error of the mean; middle row shows time courses for negative and neutral words in the attention runs; right hand shows single-participant values for averaged attention congruent and attention-incongruent conditions, with 95% confidence intervals computed at the group level; upper right hand number denotes count of participants showing effects in the valence-congruent direction; cong, averaged congruent conditions; incong, averaged incongruent conditions.

Table 9 – Post-hoc analyses for a priori ROIs. Pairwise repeated-measures t-tests ($df = 14$) for each region of interest; IFG, inferior frontal gyrus; MTG, medial temporal gyrus; SFG, superior frontal gyrus; “passive”, passive listening run, “negative” run with attention to negative words, “positive”, run with attention to positive words; “neg versus ntr” comparison of negative and neutral words; “pos versus ntr”, comparison of positive and neutral words; “neg versus pos” comparison of negative and positive words.

Region	Run type	neg versus ntr		pos versus ntr		neg versus pos	
		t	p	t	p	t	p
Words (IFG)	Passive	2.21	.044	.37	.718	2.25	.041
	Attend negative	.29	.778	−2.28	.039	3.80	.003
	Attend positive	−5.82	<.001	−.15	.882	−3.92	.002
Language (MTG)	Passive	1.41	.181	1.12	.280	−.18	.857
	Attend negative	1.42	.18	−.67	.512	1.72	.108
	Attend positive	−2.42	.030	.47	.646	−2.57	.022
Speech (STG)	passive	.10	.922	.08	.937	.01	.995
	Attend negative	−.28	.786	2.69	.017	−2.37	.033
	Attend positive	−1.02	.326	2.52	.025	−3.32	.005

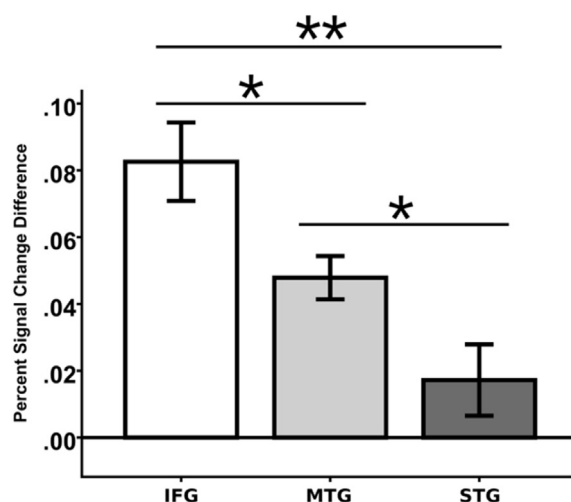


Fig. 7 – Direct comparison of magnitude of instruction-congruent signal change for the three regions of interest: Comparison of percent signal change (PSC) for the target valence congruent trials > incongruent trials contrast in IFG, MTG, and STG ROIs. Error bars denote standard error of the mean; * $p < .05$; ** $p < .01$.

shown to be less pronounced for emotional stimuli (e.g., Trapp & Kotz, 2016), which may have contributed to emotion effects in the active runs.

The areas in IFG, where the largest effects were found and where results from the whole-brain analysis converged with the ROI analysis, have previously been identified in a number of fMRI studies on emotional word processing (Canli et al., 2004; Crosson et al., 1999; Flaisch et al., 2015; Kuchinke et al., 2005; Ochsner et al., 2004). Also, present data extend previous findings of attentional highlighting by semantic cues in the IFG (Cristescu et al., 2006) that revealed activity in highly similar parts of IFG. They further complement EEG findings on pre-cueing visual selective attention to negative words that found effects on stages of early lexical access (P2) and later semantic integration (N400; Kanske, Plitschka et al., 2011). Other studies have found the IFG to contribute to the

generation of the N400 (Maess, Herrmann, Hahne, Nakamura, & Friederici, 2006) and characterized it as an integral part of the semantic system (Binder & Desai, 2011; Lau, Phillips, & Poeppel, 2008), suggesting that attention to word content in an auditory emotion evaluation task operates on semantic retrieval. Paralleling the present results, EEG source localization recently also revealed left IFG activity in a visual attention to emotional word content task, where selection of the attended valence was established via button-press rather than counting (Schindler & Kissler, 2016).

In contrast to the present results, Schindler and Kissler (2016) also found interactive effects of emotion and attention in sensory processing areas. Methodological differences between EEG and fMRI, but also differences between the auditory and visual modalities could account for the divergent patterns. In visual word processing, words are presented as a whole, facilitating instantaneous processing, whereas in auditory processing meaning unfolds gradually as the auditory sequence is processed (Kocagoncu, Clarke, Devereux, & Tyler, 2017; Marslen-Wilson & Welsh, 1978). Therefore, auditory processing of emotional word meaning may differ from processing of emotional prosody that can be extracted from very short auditory excerpts (e.g., Belin, Fillion-Bilodeau, & Gosselin, 2008) and where attention and emotion modulations in STG have been shown (e.g., Ethofer, Anders, Erb et al., 2006; Ethofer, Anders, Wiethoff et al., 2006; Grandjean et al., 2005; Sander et al., 2005). Since longer-duration environmental emotional sounds have also been shown to activate auditory cortex more than neutral environmental sounds (Plichta et al., 2011), processing of auditory emotional language content might generally operate more on semantic selection and retrieval than on the specific sensory input.

IFG activation in the present task appears consistent with semantic processes, but the role of working memory in this experiment also needs to be considered. Given that verbal working memory is known to activate left hemisphere pre-frontal structures (e.g., Braver et al., 2001), the present IFG activity could also reflect verbal working memory processes: The working memory requirement “proper” in the present study was remembering and updating the number of word occurrences rather than the verbal items themselves. This could account for the main effects of run in right SFG and left

SPL. Although the left IFG activity is in good agreement with results from previous semantic retrieval studies (e.g., [Goldberg, Perfetti, Fiez, & Schneider, 2007](#)), and perhaps more specifically, in line with the present task requirements, semantic selection ([Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997](#)), bilateral IFG activity has also been observed in arithmetic tasks ([Zago et al., 2008](#)), including activity in the vicinity of the presently reported activation.

Regarding functional differentiations in left IFG, [Liakakis, Nickel, and Seitz \(2011\)](#) in a quantitative meta-analysis of 485 neuroimaging studies targeting the functional significance of IFG activity via a designated specificity score, report three separable functional clusters of activity with different centres of gravity, pertaining to working memory (−46, 17, 22), semantics (−46, 28, 12), and empathy (−50, 25, −3). For the present attention × content interaction, peak IFG activity was at −46, 26, −12, which is on the one hand in close vicinity to all three of these functional peaks. On the other hand, however, assuming a functional gradient of activity from inferior to superior regions, the present peak would seem to align more with the semantics and empathy peaks from [Liakakis et al. \(2011\)](#) than with the working memory peak.

Clearly, speech processing in general requires working memory, such that the IFG activity observed here could be due to incremental auditory input processing and reflect the requirement of having to hold an item on-line during evaluation. Future studies will have to contrast experimentally to what extent semantic selection and retrieval are separable from working memory requirements in auditory valence decision.

We also contrasted the representation of positive and negative words during evaluation. Unlike other studies in various modalities (e.g., [Anderson et al., 2003](#); [Lewis et al., 2007](#)), there was little evidence for valence-specific regional activities in frontal cortex. A previous word reading study ([Demirakca et al., 2009](#)) likewise found considerable overlap in frontal substrates of positive and negative word processing. During silent monitoring for acoustically presented emotional words and animal and implement names, [Crosson et al. \(2002\)](#) reported category-dependent activity in the frontal executive network including motor and pre-motor areas, taken to indicate a partly content- and modality-specific division of the semantic system (for review, see [Jackson & Crosson, 2006](#)). Here, we do not address representation differences between an “emotion lexicon” and other types of, possibly modality-specific, lexica (see also [Moseley, Carota, Hauk, Mohr, & Pulvermüller, 2011](#); [Moseley & Pulvermüller, 2014](#)), but the present valence effects were relatively subtle. The post-hoc contrast of valence effects in the active runs ([Fig. 5](#)) suggests more wide-spread activity elicited by positive contents, including some regional specificity, but because none of these effects were found in the ANOVA, these activities cannot be interpreted at present. More widely distributed activity for positive contents may result from the fact that positive words typically elicit more associations than negative ones (see also [Hofmann & Jacobs, 2014](#); [Kuhlmann, Hofmann, Briesemeister, & Jacobs, 2016](#)). However, to draw firm conclusions, higher experimental power may be needed. Furthermore, valence might be coded in a non-linear pattern of neural activity by the language processing system.

The SFG, where strong interaction effects were also present, but not as firmly theoretically expected as in IFG, has been linked to evaluation, relevance detection and self-reference monitoring. SFG has been shown to be involved in evaluative decisions ([Zysset, Huber, Ferstl, & von Cramon, 2002](#)). Furthermore, during sentence classification, when participants had to evaluate spoken sentences according to happy, angry, or sad content, grammatical inflection, or intentional stance, activity in SFG was highest during affective classification ([Beaucousin et al., 2006](#)). SFG activity has been also linked to emotion regulation and attentional control ([Kanske, Heissler, Schonfelder, Bongers, & Wessa, 2011](#)). Similarly, [Sander et al. \(2005\)](#) found an interaction in SFG when an angry rather than a neutral voice was presented to the attended ear.

In the present study, effects of emotional word content during passive listening were relatively weak. Dovetailing with a study that showed diminished emotion effects in the absence of semantic processing ([Hinojosa, Méndez-Bértolo, & Pozo, 2010](#)), emotion effects increased when attention was paid to a specific valence. Of note, the ROI analysis main effect of positive content on STG activity was driven by the attended conditions, implying that a minimum of attention to content is necessary to increase sensory processing of emotional language and perhaps also indicating reduced repetition suppression for positive words as has been shown for happy faces in sensory face processing regions ([Suzuki et al., 2010](#)).

Importantly, unlike previously shown for emotional prosody ([Grandjean et al., 2005](#); [Sander et al., 2005](#)) or environmental sounds ([Plichta et al., 2011](#)), here, perceptual processing regions hardly responded to emotional content.

The STG and MTG ROIs exhibited little or no emotion effects during passive listening, but did to some extent in the active runs, favouring positive content regardless of instruction. Behaviourally, in the present study incidental memory was also best for positive words. This is in line with findings from [Herbert et al. \(2009\)](#) who reported, during visual processing, stronger responses to positive adjectives in extrastriate visual regions. As there is considerable overlap in the materials used in both studies, some hitherto unknown property of the word-set may play a role. On the other hand, the finding may also reflect a genuine effect in the processing system. Larger neural and behavioural effects for positive word content have also been reported by [Kuchinke et al. \(2005\)](#) and [Schacht & Sommer \(2009\)](#), whose work further indicates task-dependence of valence effects.

That congruency effects were strongest in frontal and high-level language areas may be explained by the current task demands, requiring allocation of processing resources to a semantic category. Accordingly, the lack of interaction effects in STG could reflect this region's involvement in prosody and early auditory processing rather than semantic retrieval. Whereas previous studies using a dichotic listening paradigm to investigate how processing of emotional prosody is modulated by attention found no emotion–attention interaction in early auditory processing regions ([Grandjean et al., 2005](#); [Sander et al., 2005](#)), during visual word processing emotion and attention effects have been found at least in secondary ([Schindler & Kissler, 2016](#)), if not in primary ([Trauer et al., 2012](#); [2015](#)) visual regions, perhaps reflecting a genuine

difference between the two modalities. Indeed, a study investigating the cerebral sources of the typically emotion-sensitive Early Posterior Negativity (EPN) event-related potential during auditory word processing, localized auditory EPN sources in the superior parietal lobule, but not in early auditory processing regions (Jaspers-Fayer, Ertl, Leicht, Leupelt, & Mulert, 2012). Conversely, a recent study investigating competitive emotion and attention effects in visual word and picture processing (emotional words were overlaid on emotional pictures and participants had to attend to either stimulus type), found main effects for emotional content in left IFG, but main effects of attention to words in left extrastriate visual areas (Flaisch et al., 2015), underscoring that emotion and attention can interact in a variety of ways that are not yet fully understood.

Temporal dynamics also need to be considered. EEG data show that emotional material can be processed rapidly (e.g., Keuper et al., 2013; Kissler & Herbert, 2013; Kissler et al., 2007; Pourtois, 2004; Stolarova, Keil, & Moratti, 2005) and early and late responses can differ qualitatively (Pourtois, Spinelli, Seeck, & Vuilleumier, 2010; Schindler, Wegrzyn, Steppacher, & Kissler, 2015; Schindler & Kissler, 2016; Schupp et al., 2007). In fMRI studies, such timing differences may be obscured and transient early effects in perceptual areas may not translate into BOLD effects. On the other hand, genuine differences between experimental tasks, or the auditory and visual modalities may exist regarding the locus of emotion–attention interactions. Although the absence of task-congruent STG and MTG effects could be partly due to lack of experimental power and future studies with more stimuli and more participants may reveal such effects, the present comparison across regions indicates that IFG exhibits at least relatively greatest sensitivity. Overall, the data pattern seems most consistent with the notion that a given word's meaning was selected and retrieved via left IFG and further evaluated in left SFG. During this process the item will have to be held in working memory, potentially again recruiting IFG.

In summary, the present study identified interactions of emotion and attention in prefrontal brain areas, but the nature of his relationship should be further specified.

We found reliable task-driven amplification of valence-congruent emotional word processing in higher-level language-related brain areas in IFG, close to Broca's area, as well as in SFG. These results identify hubs in the brain where emotional and cognitive processes overlap in auditory word processing when prosody is neutral.

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Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.cortex.2017.08.018>.

REFERENCES

- Anderson, A. K., Christoff, K., Stappen, I., Panitz, D., Ghahremani, D. G., Glover, G., et al. (2003). Dissociated neural representations of intensity and valence in human olfaction. *Nature Neuroscience*, 6, 196–202.
- Ashburner, J., & Friston, K. J. (2005). Unified segmentation. *NeuroImage*, 26, 839–851.
- Beaucousin, V., Lacheret, A., Turbelin, M.-R., Morel, M., Mazoyer, B., & Tzourio-Mazoyer, N. (2006). fMRI study of emotional speech comprehension. *Cerebral Cortex*, 17, 339–352.
- Belin, P., Fillion-Bilodeau, S., & Gosselin, F. (2008). The montreal affective voices: A validated set of nonverbal affect bursts for research on auditory affective processing. *Behavior Research Methods*, 40(2), 531–539.
- Binder, J. R., & Desai, R. H. (2011). The neurobiology of semantic memory. *Trends in Cognitive Sciences*, 15, 527–536.
- Bradley, M. M., Keil, A., & Lang, P. J. (2012). Orienting and emotional perception: Facilitation, attenuation, and interference. *Frontiers in Psychology*, 3.
- Bradley, M. M., & Lang, P. J. (1994). Measuring emotion: The self-assessment manikin and the semantic differential. *Journal of Behavior Therapy and Experimental Psychiatry*, 25, 49–59.
- Braver, T. S., Barch, D. M., Kelley, W. M., Buckner, R. L., Cohen, N. J., Miezin, F. M., et al. (2001). Direct comparison of prefrontal cortex regions engaged by working and long-term memory tasks. *NeuroImage*, 14(1), 48–59.
- Brett, M., Anton, J., Valabregue, R., & Poline, J. (2002). Region of interest analysis using an SPM toolbox. In *Present. 8th Int. Conf. Funct. Mapp. Hum. Brain June 2–6; Sendai, Japan*.
- Canli, T., Sivers, H., Thomason, M. E., Whitfield-Gabrieli, S., Gabrieli, J. D. E., & Gotlib, I. H. (2004). Brain activation to emotional words in depressed vs healthy subjects. *NeuroReport*, 15, 2585–2588.
- 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, 167–177.
- Corbetta, M., Miezin, F. M., Dobmeyer, S., Shulman, G. L., & Petersen, S. E. (1990). Attentional modulation of neural processing of shape, color, and velocity in humans. *Science*, 248, 1556–1559.
- Corbetta, M., Miezin, F. M., Dobmeyer, S., Shulman, G. L., & Petersen, S. E. (1991). Selective and divided attention during visual discriminations of shape, color, and speed: Functional anatomy by positron emission tomography. *The Journal of Neuroscience*, 11, 2383–2402.
- Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience*, 3(3), 201–215.
- Cristescu, T. C., Devlin, J. T., & Nobre, A. C. (2006). Orienting attention to semantic categories. *NeuroImage*, 33, 1178–1187.
- Cristescu, T. C., & Nobre, A. C. (2008). Differential modulation of word recognition by semantic and spatial orienting of attention. *Journal of Cognitive Neuroscience*, 20, 787–801.
- Crosson, B., Cato, M. A., Sadek, J. R., Gökçay, 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(05), 607–622.
- Crosson, B., Radonovich, K., Sadek, J. R., Gokcay, D., Bauer, R. M., Fischler, I. S., et al. (1999). Left-hemisphere processing of emotional connotation during word generation. *NeuroReport*, 10, 2449–2455.
- Demirakca, T., Herbert, C., Kissler, J., Ruf, M., Wokrina, T., & Ende, G. (2009). Overlapping neural correlates of reading

- emotionally positive and negative adjectives. *The Open Neuroimaging Journal*, 3, 54.
- 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, 580–587.
- Ethofer, T., Anders, S., Wiethoff, S., Erb, M., Herbert, C., Saur, R., et al. (2006). Effects of prosodic emotional intensity on activation of associative auditory cortex. *NeuroReport*, 17(3), 249–253.
- Ferrari, V., Codispoti, M., Cardinale, R., & Bradley, M. M. (2008). Directed and motivated attention during processing of natural scenes. *Journal of Cognitive Neuroscience*, 20(10), 1753–1761.
- Flaisch, T., Imhof, M., Schmälzle, R., Wentz, K. U., Ibach, B., & Schupp, H. T. (2015). Implicit and explicit attention to pictures and words: An fMRI-study of concurrent emotional stimulus processing. *Frontiers in Psychology*, 6.
- Friston, K. J., Rotshtein, P., Geng, J. J., Sterzer, P., & Henson, R. N. (2006). A critique of functional localisers. *NeuroImage*, 30, 1077–1087.
- Goldberg, R. F., Perfetti, C. A., Fiez, J. A., & Schneider, W. (2007). Selective retrieval of abstract semantic knowledge in left prefrontal cortex. *Journal of Neuroscience*, 27(14), 3790–3798.
- Grandjean, D., Sander, D., Pourtois, G., Schwartz, S., Seghier, M. L., Scherer, K. R., et al. (2005). The voices of wrath: Brain responses to angry prosody in meaningless speech. *Nature Neuroscience*, 8, 145–146.
- Haxby, J. V., Hoffman, E. A., & Gobbini, M. I. (2000). The distributed human neural system for face perception. *Trends in Cognitive Sciences*, 4, 223–233.
- Herbert, C., Ethofer, T., Anders, S., Junghofer, M., Wildgruber, D., Grodd, W., et al. (2009). Amygdala activation during reading of emotional adjectives—an advantage for pleasant content. *Social Cognitive and Affective Neuroscience*, 4, 35–49 [electronic Resource].
- Herbert, C., Junghofer, M., & Kissler, J. (2008). Event related potentials to emotional adjectives during reading. *Psychophysiology*, 45(3), 487–498.
- Hinojosa, J. A., Méndez-Bértolo, C., & Pozo, M. A. (2010). Looking at emotional words is not the same as reading emotional words: Behavioral and neural correlates. *Psychophysiology*, 47(4), 748–757.
- Hofmann, M. J., & Jacobs, A. M. (2014). Interactive activation and competition models and semantic context: From behavioral to brain data. *Neuroscience and Biobehavioral Reviews*, 46, 85–104.
- Jackson, A. C., & Crosson, B. (2006). Emotional connotation of words: Role of emotion in distributed semantic systems. *Progress in Brain Research*, 156, 205–216.
- Jäncke, L., Buchanan, T. W., Lutz, K., & Shah, N. J. (2001). Focused and nonfocused attention in verbal and emotional dichotic listening: An FMRI study. *Brain and Language*, 78(3), 349–363.
- Jaspers-Fayer, F., Ertl, M., Leicht, G., Leupelt, A., & Mulert, C. (2012). Single-trial EEG–fMRI coupling of the emotional auditory early posterior negativity. *NeuroImage*, 62(3), 1807–1814.
- Kanske, P., Heissler, J., Schonfelder, S., Bongers, A., & Wessa, M. (2011). How to regulate Emotion? Neural networks for reappraisal and distraction. *Cerebral Cortex*, 21, 1379–1388.
- Kanske, P., Plitschka, J., & Kotz, S. A. (2011). Attentional orienting towards emotion: P2 and N400 ERP effects. *Neuropsychologia*, 49, 3121–3129.
- Keuper, K., Zwanzger, P., Nordt, M., Eden, A., Laeger, I., Zwitterlood, P., et al. (2014). How ‘love’ and ‘hate’ differ from ‘sleep’: Using combined electro/magnetoencephalographic data to reveal the sources of early cortical responses to emotional words. *Human Brain Mapping*, 35(3), 875–888.
- Keuper, K., Zwitterlood, P., Rehbein, M. A., Eden, A. S., Laeger, I., Junghöfer, M., et al. (2013). Early prefrontal brain responses to the hedonic quality of emotional words – a simultaneous EEG and MEG study. *PLoS One*, 8, e70788.
- Kissler, J., & Herbert, C. (2013). Emotion, Etmnooi, or Emitoon? – Faster lexical access to emotional than to neutral words during reading. *Biological Psychology*, 92, 464–479.
- Kissler, J., Herbert, C., Peyk, P., & Junghofer, M. (2007). Buzzwords: Early cortical responses to emotional words during reading. *Psychological Science*, 18, 475–480.
- Kissler, J., Herbert, C., Winkler, I., & Junghofer, M. (2009). Emotion and attention in visual word processing—an ERP study. *Biological Psychology*, 80, 75–83.
- Kocagoncu, E., Clarke, A., Devereux, B. J., & Tyler, L. K. (2017). Decoding the cortical dynamics of sound-meaning mapping. *Journal of Neuroscience*, 37(5), 1312–1319. <http://dx.doi.org/10.1523/JNEUROSCI.2858-16.2016>.
- Kuchinke, L., Jacobs, A. M., Grubich, C., Võ, M. L.-H., Conrad, M., & Herrmann, M. (2005). Incidental effects of emotional valence in single word processing: An fMRI study. *NeuroImage*, 28, 1022–1032.
- Kuhlmann, M., Hofmann, M. J., Briesemeister, B. B., & Jacobs, A. M. (2016). Mixing positive and negative valence: Affective-semantic integration of bivalent words. *Scientific Reports*, 6, 30718.
- Lang, P. J., Bradley, M. M., & Cuthbert, B. N. (1992). A motivational analysis of emotion: Reflex-cortex connections. *Psychological Science*, 3, 44–49.
- Lau, E. F., Phillips, C., & Poeppel, D. (2008). A cortical network for semantics: (de)constructing the N400. *Nature Reviews Neuroscience*, 9, 920–933.
- Lewis, R. S., Weekes, N. Y., & Wang, T. H. (2007). The effect of a naturalistic stressor on frontal EEG asymmetry, stress, and health. *Biological Psychology*, 75, 239–247.
- Liakakis, G., Nickel, J., & Seitz, R. J. (2011). Diversity of the inferior frontal gyrus—a meta-analysis of neuroimaging studies. *Behavioural Brain Research*, 225(1), 341–347.
- Maess, B., Herrmann, C. S., Hahne, A., Nakamura, A., & Friederici, A. D. (2006). Localizing the distributed language network responsible for the N400 measured by MEG during auditory sentence processing. *Brain Research*, 1096, 163–172.
- Marslen-Wilson, W. D., & Welsh, A. (1978). Processing interactions and lexical access during word recognition in continuous speech. *Cognitive Psychology*, 10(1), 29–63.
- Mazaika, P. K., Whitfield, S., & Cooper, J. C. (2005). Detection and repair of transient artifacts in fMRI data. *NeuroImage*, 26, S36.
- Moseley, R., Carota, F., Hauk, O., Mohr, B., & Pulvermüller, F. (2011). A role for the motor system in binding abstract emotional meaning. *Cerebral Cortex*, 22(7), 1634–1647.
- Moseley, R. L., & Pulvermüller, F. (2014). Nouns, verbs, objects, actions, and abstractions: Local fMRI activity indexes semantics, not lexical categories. *Brain and Language*, 132, 28–42.
- Nakic, M., Smith, B. W., Busis, S., Vythilingam, M., & Blair, R. J. R. (2006). The impact of affect and frequency on lexical decision: The role of the amygdala and inferior frontal cortex. *NeuroImage*, 31, 1752–1761.
- Narumoto, J., Okada, T., Sadato, N., Fukui, K., & Yonekura, Y. (2001). Attention to emotion modulates fMRI activity in human right superior temporal sulcus. *Cognitive Brain Research*, 12, 225–231.
- Ochsner, K. N., Ray, R. D., Cooper, J. C., Robertson, E. R., Chopra, S., Gabrieli, J. D. E., et al. (2004). For better or for worse: Neural systems supporting the cognitive down- and up-regulation of negative emotion. *NeuroImage*, 23, 483–499.
- Plichta, M. M., Gerdes, A. B., Alpers, G. W., Harnisch, W., Brill, S., Wieser, M. J., et al. (2011). Auditory cortex activation is modulated by emotion: A functional near-infrared spectroscopy (fNIRS) study. *NeuroImage*, 55(3), 1200–1207.
- Poldrack, R. (2006). Can cognitive processes be inferred from neuroimaging data? *Trends in Cognitive Sciences*, 10, 59–63.
- Pourtois, G. (2004). Electrophysiological correlates of rapid spatial orienting towards fearful faces. *Cerebral Cortex*, 14, 619–633.
- Pourtois, G., Spinelli, L., Seeck, M., & Vuilleumier, P. (2010). Temporal precedence of emotion over attention modulations in the lateral amygdala: Intracranial ERP evidence from a

- patient with temporal lobe epilepsy. *Cognitive, Affective & Behavioral Neuroscience*, 10, 83–93.
- Roskies, A. L., Fiez, J. A., Balota, D. A., Raichle, M. E., & Petersen, S. E. (2001). Task-dependent modulation of regions in the left inferior frontal cortex during semantic processing. *Journal of Cognitive Neuroscience*, 13(6), 829–843.
- Sabatinelli, D., Bradley, M. M., Lang, P. J., Costa, V. D., & Versace, F. (2007). Pleasure rather than salience activates human nucleus accumbens and medial prefrontal cortex. *Journal of Neurophysiology*, 98, 1374–1379.
- 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.
- Schacht, A., & Sommer, W. (2009). Time course and task dependence of emotion effects in word processing. *Cognitive, Affective, & Behavioral Neuroscience*, 9(1), 28–43.
- Scherer, K. R. (2013). The nature and dynamics of relevance and valence appraisals: Theoretical advances and recent evidence. *Emotion Review*, 5(2), 150–162.
- Schindler, S., & Kissler, J. (2016). Selective visual attention to emotional words: Early parallel frontal and visual activations followed by interactive effects in visual cortex. *Human Brain Mapping*, 37(10), 3575–3587.
- Schindler, S., Wegryzn, M., Steppacher, I., & Kissler, J. (2015). Perceived communicative context and emotional content amplify visual word processing in the fusiform gyrus. *Journal of Neuroscience*, 35(15), 6010–6019.
- Schirmer, A., Zysset, S., Kotz, S. A., & von Cramon, D. Y. (2004). Gender differences in the activation of inferior frontal cortex during emotional speech perception. *NeuroImage*, 21(3), 1114–1123.
- Schoenfeld, M. A., Hopf, J.-M., Merkel, C., Heinze, H.-J., & Hillyard, S. A. (2014). Object-based attention involves the sequential activation of feature-specific cortical modules. *Nature Neuroscience*, 17, 619–624.
- Schupp, H. T., Flaisch, T., Stockburger, J., & Junghöfer, M. (2006). Emotion and attention: Event-related brain potential studies. *Progress in Brain Research*, 156, 31–51.
- Schupp, H. T., Junghöfer, M., Weike, A. I., & Hamm, A. O. (2003). Attention and emotion: An ERP analysis of facilitated emotional stimulus processing. *NeuroReport*, 14, 1107–1110.
- 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(2), 189.
- Schupp, H. T., Stockburger, J., Codispoti, M., Junghofer, M., Weike, A. I., & Hamm, A. O. (2007). Selective visual attention to emotion. *The Journal of Neuroscience*, 27, 1082–1089.
- Shattuck, D. W., Mirza, M., Adisetiyo, V., Hojatkashani, C., Salamon, G., Narr, K. L., et al. (2008). Construction of a 3D probabilistic atlas of human cortical structures. *NeuroImage*, 39, 1064–1080.
- Small, D. M., Gregory, M. D., Mak, Y. E., Gitelman, D., Mesulam, M. M., & Parrish, T. (2003). Dissociation of neural representation of intensity and affective valuation in human gustation. *Neuron*, 39, 701–711.
- Smith, S. M. (2002). Fast robust automated brain extraction. *Human Brain Mapping*, 17, 143–155.
- Stolarova, M., Keil, A., & Moratti, S. (2005). Modulation of the C1 visual event-related component by conditioned stimuli: Evidence for sensory plasticity in early affective perception. *Cerebral Cortex*, 16, 876–887.
- Suzuki, A., Goh, J. O., Hebrank, A., Sutton, B. P., Jenkins, L., Flicker, B. A., et al. (2010). Sustained happiness? Lack of repetition suppression in right-ventral visual cortex for happy faces. *Social Cognitive and Affective Neuroscience*, 6(4), 434–441.
- Thompson-Schill, S. L., D'Esposito, M., Aguirre, G. K., & Farah, M. J. (1997). Role of left inferior prefrontal cortex in retrieval of semantic knowledge: A re-evaluation. *Proceedings of the National Academy of Sciences*, 94(26), 14792–14797.
- Trapp, S., & Kotz, S. A. (2016). Predicting affective information—An evaluation of repetition suppression effects. *Frontiers in Psychology*, 7.
- Trauer, S. M., Andersen, S. K., Kotz, S. A., & Müller, M. M. (2012). Capture of lexical but not visual resources by task-irrelevant emotional words: A combined ERP and steady-state visual evoked potential study. *NeuroImage*, 60(1), 130–138.
- Trauer, S. M., Kotz, S. A., & Müller, M. M. (2015). Emotional words facilitate lexical but not early visual processing. *BMC Neuroscience*, 16(1), 89.
- Yarkoni, T., Poldrack, R. A., Nichols, T. E., Van Essen, D. C., & Wager, T. D. (2011). Large-scale automated synthesis of human functional neuroimaging data. *Nature Methods*, 8, 665–670.
- Zago, L., Petit, L., Turbelin, M. R., Andersson, F., Vigneau, M., & Tzourio-Mazoyer, N. (2008). How verbal and spatial manipulation networks contribute to calculation: An fMRI study. *Neuropsychologia*, 46(9), 2403–2414.
- Zysset, S., Huber, O., Ferstl, E., & von Cramon, D. Y. (2002). The anterior frontomedian cortex and evaluative judgment: An fMRI study. *NeuroImage*, 15, 983–991.