

A network analysis of audiovisual affective speech perception

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A NETWORK ANALYSIS OF AUDIOVISUAL AFFECTIVE SPEECH PERCEPTION

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Abstract—In this study we were interested in the neural system supporting the audiovisual (AV) integration of emotional expression and emotional prosody. To this end normal participants were exposed to short videos of a computer-animated face voicing emotionally positive or negative words with the appropriate prosody. Facial expression of the face was either neutral or emotionally appropriate. To reveal the neural network involved in affective AV integration, standard univariate analysis of functional magnetic resonance (fMRI) data was followed by a random-effects Granger causality mapping (RFX-GCM). The regions that distinguished emotional from neutral facial expressions in the univariate analysis were taken as seed regions. In trials showing emotional expressions compared to neutral trials univariate analysis showed activation primarily in bilateral amygdala, fusiform gyrus, middle temporal gyrus/superior temporal sulcus and inferior occipital gyrus. When employing either the left amygdala or the right amygdala as a seed region in RFX-GCM we found connectivity with the right hemispheric fusiform gyrus, with the indication that the fusiform gyrus sends information to the Amygdala. These results led to a working model for face perception in general and for AV-affective integration in particular which is an elaborated adaptation of existing models. © 2013 IBRO. Published by Elsevier Ltd. All rights reserved.

Key words: audiovisual speech, emotion, facial affect perception, amygdala, Granger causality.

INTRODUCTION

Audiovisual (AV) integration in the perception of speech is the rule rather than the exception. For example, the presence of congruent visual (V) information leads to a considerable improvement of intelligibility under noisy conditions (Sumby and Pollack, 1954; Schwartz et al.,

2004; Ross et al., 2007) which can be in the range of 10 dB. On the other hand, incongruent V information may induce the striking McGurk illusion (McGurk and MacDonald, 1976) during which syllables are perceived that are neither heard nor seen (e.g., percept/da/, auditory information: /ba/, visual information/ga/). This illusion suggests that AV integration during speech perception is a rather automatic process.

A number of recent studies have addressed the neural underpinnings of AV integration in speech perception and consistently found two different brain areas, the inferior frontal gyrus (IFG) and the superior temporal sulcus (STS) (Calvert et al., 2000; Calvert and Campbell, 2003; Sekiyama et al., 2003; Wright et al., 2003; Barraclough et al., 2005; Szycik et al., 2008, 2009, 2012). Interactions of the STS and IFG are captured by the AV-motor integration model of speech perception (Skipper et al., 2007). This model posits the formation of a sensory hypothesis in STS which is further specified in terms of the motor goal of the articulatory movements established in the pars opercularis of the IFG. While the advantage of AV information over unimodal A or V information for the perception of speech is clearly established, the question arises whether bimodal AV information is also advantageous for other types of information. Indeed, it has been shown that the identity of a speaker might be recognized from both visual and auditory information but that there is a strong interaction between these kinds of information (von Kriegstein et al., 2005; Blank et al., 2011).

The topic of the present study is AV integration of affective information transmitted by the voice or face of a speaker. (Scherer, 2003) compared the recognition accuracy for vocal and facial emotions as they had been obtained in a number of studies either using unimodal vocal expression (previously reviewed by Scherer et al. (2001)) or unimodal facial expression (previously reviewed by Ekman (1994)). If one limits the analysis to studies of Western faces and voices, recognition accuracy for the emotions anger, fear, joy, sadness, disgust, and surprise ranged between 31% (disgust) and 77% (anger) for vocal emotions and between 77% (fear) and 95% (joy) for facial expressions. Thus, for both modalities recognition for most emotions is far from perfect. The question therefore arises whether the combination of both types of information will increase recognition accuracy. Indeed, a number of studies have revealed clear behavioral face–voice integration effects for affective stimuli: for example, de Gelder and

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Abbreviations: AV, audiovisual; BOLD, blood oxygen level dependent; EMO, emotional; fMRI, functional magnetic resonance; FOV, field of view; IFG, inferior frontal gyrus; MTG, middle temporal gyrus; NEU, neutral; RFX-GCM, random effects Granger causality mapping; STS, superior temporal sulcus; V, visual; VOI, volume of interest.

Vroomen (2000) obtained affective ratings of facial stimuli that were morphed to represent a continuum between two facial expressions. These ratings were clearly influenced by the concurrent presentation of an affective vocalization, even under instructions to ignore the voice. A comparable effect was also obtained for ratings of affect for the vocalizations. Further research revealed that crossmodal interaction occurs even, if facial expressions are presented subliminally (de Gelder et al., 2002). In a similar vein, Collignon et al. (2008) found that the irrelevant information affected processing, even if participants were asked to ignore one sensory modality, thus further suggesting mandatory integration of visual and auditory emotional information. Further evidence for early interaction comes from electrophysiological studies. Incongruent pairings of an affective vocalization and a facial emotion have been found to evoke a negativity akin to the mismatch negativity around 180 ms (de Gelder et al., 1999), whereas in another study affectively congruent voice/face pairings gave rise to an enhanced amplitude of the auditory N1 response (Pourtois et al., 2000).

Neuroimaging has been used to shed light on the functional neuroanatomy of the processing of affective facial and vocal information. Facial expressions, even when presented subliminally, have been shown to activate the amygdala with the greatest responses observed for expressions of fear (Breiter et al., 1996; Morris et al., 1996; Gelder et al., 1997; Whalen et al., 2001; Williams, 2002; Noesselt et al., 2005; Vuilleumier and Pourtois, 2007). Interestingly, robust activations for the amygdala have been observed when emotional processing is implicit, whereas explicit emotion recognition often leads to a deactivation of the amygdala (Critchley et al., 2000). Other regions that have been found with regard to the processing of facial expressions include the orbitofrontal cortex which is activated by fearful (Vuilleumier et al., 2001), angry but not sad expressions (Blair et al., 1999). The latter dissociation of the processing of angry and sad expressions has also been found for the anterior cingulate cortex (Blair et al., 1999). Adolphs (2002a,b) has summarized the imaging and lesion findings and has suggested a neuroanatomical model of affect recognition from facial expressions.

With regard to the processing of voice, the seminal study of Belin et al. (2002) suggested a prominent role of the STS. Even earlier, the amygdala has been implicated by a number of studies for the processing of affective vocalizations (Phillips et al., 1998; Morris et al., 1999). Buchanan et al. (2000) compared the detection of emotional and semantic properties of stimuli with the former giving rise to activity in the right inferior frontal lobe. Adolphs et al. (2002) found that the right frontoparietal cortex, left frontal operculum and bilateral frontal polar cortex (area 10) are critical to recognizing emotion from prosody. Investigating vocal attractiveness as a paralinguistic cue during social interactions, Bestelmeyer et al. (2012) similarly found that inferior frontal regions in addition to voice-sensitive auditory areas were strongly correlated with implicitly perceived

vocal attractiveness. In an effort to distinguish the neural representation of different kinds of emotion, Ethofer et al. (2009) presented pseudowords spoken with different affective connotation (anger, sadness, neutral, relief, and joy) and subjected their functional magnetic resonance (fMRI) activations to multivariate pattern analysis. These authors successfully decoded the different vocal emotions from fMRI in bilateral voice-sensitive areas.

With regard to crossmodal integration of emotional information, a first fMRI study required participants to categorize static facial expression as fearful or happy while simultaneously presented emotional vocalizations were to be ignored (Dolan et al., 2001). Activation of the left amygdala was stronger when both, facial expression and voice signaled fear, thus suggesting a role of the amygdala in the crossmodal integration of fear. Building on this early study, Ethofer et al. (2006a,b) found that the crossmodal bias observed in affective ratings of fear correlated with activity in the amygdalae. Applying the criterion of supra-additivity (i.e., the response to face–voice pairings in combination is greater than the sum of the activations to each of the modalities presented separately), Pourtois et al. (2005) delineated the middle temporal gyrus (MTG) as a core region for the crossmodal integration of a variety of emotions. While these earlier studies used static facial expressions, Kreifelts et al. (2007) employed dynamic video-clips and tested a number of different emotional expressions. The bilateral posterior STS region, which has also been highlighted for AV integration in general, was found to be important for affective integration in this study. In a further study (Kreifelts et al., 2009) these authors found evidence for a segregation of the STS region into a voice-sensitive region in the trunk section, a region with maximum face sensitivity in the posterior terminal ascending branch, and an AV integration area for emotional signals at the bifurcation of the STS. Similar to the present study, Klasen et al. (2011) used computer-generated emotional faces and voices to assess the neural effects of emotional congruency during an explicit emotional classification task. Congruent AV stimuli led to activation in amygdala, insula, ventral posterior cingulate, temporo-occipital, and auditory cortex, whereas incongruent stimuli gave rise to activations in frontoparietal regions as well as the caudate nucleus bilaterally.

In the present investigation we were interested in the neural system supporting the AV integration of emotional face information and emotional prosody. Normal participants were exposed to short videos of a computer-animated face voicing emotionally positive or negative words with the appropriate prosody. Facial expression was either neutral or emotionally appropriate. To reveal the neural network involved in AV integration, standard univariate analysis of fMRI data was followed by a connectivity analysis (Granger causality mapping (GCM); Roebroek et al., 2005; Valdes-Sosa et al., 2011; Stephan and Roebroek, 2012). GCM was introduced as it allows, similar to dynamic causal modeling (Stephan and Roebroek,

2012), to investigate directed influences of one brain area on others. An advantage of the particular implementation of GCM used in this paper is that no a priori model about the number of brain areas and their connections has to be used. GCM has been applied successfully to fMRI analysis in a number of studies (e.g., Formisano et al., 2002; Bressler et al., 2008; Sridharan et al., 2008). We predicted to find enhanced neural activity in the STS for emotionally appropriate relative to neutral animations and a causal influence of the auditory cortex and visual areas related to the processing of affective facial information in the STS.

EXPERIMENTAL PROCEDURE

All procedures were approved by the ethics review board of the University of Magdeburg, the affiliation of the first and last author at the time of the study. The study was performed in compliance with the Declaration of Helsinki.

Participants and procedure

The data of 14 right-handed, neurologically healthy participants with normal or corrected-to-normal visual acuity were used (8 women, age range 19–24 years). Data of six additional participants had to be discarded either due to extensive head-movements ($n = 5$) or problems with contact lenses ($n = 1$).

Stimuli

A total of 60 concrete German nouns with a positive and 60 concrete nouns with a negative affective connotation were selected from the Berlin Affective Word List (Vo et al., 2006) which comprises 2200 German words assessed by 88 normal German speaking volunteers for emotional valence (on a 7-point scale ranging from –3 to 3) and imageability (on a 7-point scale ranging from 1 to 7). Selected positive words had a mean rating of 1.83 (SD 0.38) and negative words had a mean rating of –1.83 (SD 0.35). Positive and negative words were matched for imageability (average: positive 4.52; SD 1.43; negative 4.29; SD 1.03).

Short video-clips of an animated, computer-generated, photo-realistic face with synchronized lip-movements pronouncing the words were produced using the software Maya (<http://www.autodesk.com>); for examples see [Supplemental Material](#)). The quality of the animations is comparable with modern special effects animations used in the film industry. The emotional expression of the computer-animated face was assessed by a group of 10 young participants (5 women, age 19–28). These were asked to rate the valence of the facial expression on a scale ranging from –5 (very negative) to +5 (very positive). Emotionally negative/positive expressions were judged to be –3.4/3.1.

The words were spoken by a professional voice actor using affective prosody that matched the emotional valence (positive or negative) of the word. Again, 10 young participants judged the emotional valence of the

intonation of the actor on a scale ranging from –5 (very negative) to +5 (very positive). A mean rating of the negatively/positively spoken words of –3.1/2.6 was obtained.

The face of the animated character either showed a modulated emotional expression (henceforth: EMO) or remained neutral (NEU). In order to avoid item effects, a neutral and an emotionally modulated animation was made of each word. The participants were shown 50% of the words with a neutral animation and the remainder with an emotional animation. The animation types were counterbalanced across subjects such that each item was equally tested in both animation types.

All animations lasted 1880 ms corresponding to 47 video frames and were displayed with a frame rate of 25 frames per second. The animations had a resolution of 1024×768 pixels, an aspect ratio of 4:3, and 24 bit sample size. The corresponding audio signal had 16-bit resolution.

Because a computer-animated face was used, it could be ensured that EMO and NEU conditions were matched in terms of general movement, head movement and eye movement of the animated torso. The lip movement was always in perfect synchrony with the auditory stimulation of the word.

The animations were presented using Presentation software (www.neurobehavioralsystems.com) via a projector that rear-projected the stimuli onto a screen which was viewed by the participants with the aid of a mirror mounted on the head coil. The distance to screen was about 59 cm and the width of projection was 32.5 cm. Audio-information was presented via MRI compatible electrodynamic headphones integrated into earmuffs to reduce residual background scanner noise (Baumgartner et al., 2006). The sound level of stimuli was individually adjusted to achieve good audibility during data acquisition.

Functional MR images were acquired in a slow event-related design. In order to synchronize acquisition timing between scanner and stimulus-PC, the start of each trial was initiated by an external pulse from the scanner. At the beginning of the run a fixation cross was presented for 10 s, followed by 120 trials. Each trial comprised an animation (stimulus), followed by a fixation cross of various durations (6–8 times TR). The order in which the animations were presented was randomized across conditions for each participant. Each participant saw 60 EMO (emotional facial expression congruently paired with 30 negative and 30 positive words) and 60 NEU (neutral facial expression paired with 30 negative and 30 positive words) videos. The functional run took 23 min and was followed by the acquisition of the structural data set.

Participants were asked to fixate the cross before and after each animation and to watch the videos in order to perform a subsequent memory test. In this memory test the stimuli were presented again randomly intermixed with an equal number of new videos of the same kind but animating different words. The participants had to decide for each stimulus whether it had been presented before or not.

fMRI acquisition and analysis

Images were acquired on a 3T Siemens Magnetom Trio head scanner (Siemens Medical Systems, Erlangen, Germany) using a standard 8 channel head coil. Twenty-six oblique axial slices were acquired (in-plane resolution: 3.5×3.5 mm, slice thickness: 3.2 mm, interslice distance 0.8 mm) covering almost the entire cortical volume using an echo planar imaging sequence (TR = 1600 ms, field of view (FOV) 224 mm, TE = 30 ms, matrix size: 64×64 , flip angle 75°). In total, 851 volumes were acquired of which the first 2 were discarded to allow for T1 saturation. Functional slices were aligned to a high-resolution T1-weighted anatomical scan acquired on the same scanner running a three-dimensional T1-fast-low-angle shot sequence lasting 9 min and 50 s (MPRAGE, 192 slices, slice thickness 1 mm, TR 2500 ms; TE 4.77 ms; FA 7° ; FOV 256 mm; matrix 256×256).

Using BrainVoyager QX (Brain Innovation, Maastricht, The Netherlands) functional data were slice scan-time corrected, and corrected for motion in three dimensions. Subsequently, linear drifts were removed from the signal and data were high-pass filtered to remove slow frequency drifts up to 3 cycles per time course. Data were spatially smoothed with a Gaussian kernel of 6 mm (FWHM) and aligned to the last volume of the dataset, which was closest in time to the recording of the structural scan. The correction for movement during the run was done using a bi-cubic spline interpolation allowing the algorithm maximally 300 iterations for volume movement parameter estimation. Functional data were aligned to the high-resolution anatomical images, morphed to fit Talairach dimensions (Talairach and Tournoux, 1988) and combined into a 4-dimensional (x, y, z , time) dataset for each run and each subject.

Univariate statistical analysis

Trials with emotional expression and without emotional expression were compared using random effects general linear model (RFX-GLM) analysis: in a first level, a standard GLM was used to estimate the beta values (summary statistics) for each subject and condition (level 1), which were then entered to the

second level analysis as the dependent variable. At this level of analysis the main effect of animation was tested.

The correction for multiple comparisons was performed using cluster-size thresholding. The procedure started with setting a threshold (manually) for the map relative to the contrast of interest with a $p < 0.005$ (uncorrected). Next, the intrinsic smoothness of the resulting map was evaluated automatically (Forman et al., 1995; Goebel et al., 2006). The final result was a minimum cluster size threshold set for the current map to achieve a corrected p value of < 0.005 .

Connectivity analysis

To reveal the brain network underlying the perception of affective facial expression GCM, a vector autoregressive modeling technique, was used to define effective and/or functional connectivity (Goebel et al., 2003; Roebroeck et al., 2005). Briefly, the average blood oxygen level-dependent (BOLD) response collected across time from a volume of interest (VOI) make up a vector time series, $x_i(t)$, where t represents time and i denotes the VOI. To identify and characterize effective connectivity in GCM, it is assumed that the time series $x(t)$ is a function of its own past $x(t-l, \dots, t-p)$ and possibly of the past of another VOI or single voxel $y(t-l, \dots, t-p)$. Therefore, it can be stated that if there is causality between x and y , the present value of x can be better predicted using the information of both time series $x(t)$ and $y(t)$ compared with solely using the information in time series $x(t)$. Furthermore, the number of time series that can be used to predict the current value x can be more than two. This method, unlike some other methods for testing connectivity, does not require the a priori definition of a network including all brain areas to be tested. On the basis of Granger causality, the existence and direction of influence on and from the seeding region in respect to the rest of the brain can be investigated. In addition to directed causality the instantaneous influence (correlation) between $x(t)$ and $y(t)$ can be detected when values $x(t)$ improve predictions of synchronous values $y(t)$ (or vice versa, instantaneous correlation is symmetric), taking into account all other relevant sources of influence (at the very least the past of both x and y). Note, therefore, that the instantaneous correlation reported here is subtly

Table 1. Univariate analysis emotional expression (EMO) > neutral expression (NEU)

Region of activation	Laterality	Coordinates	Voxels	BA	t Value	p Value
<i>Main effect EMO > NEU</i>						
Amygdala	L	–21 –11 –9	516		4.2028	0.0018
Amygdala	R	18 –12 –10	270		3.9989	0.0021
Middle temporal gyrus	L	–49 –63 1	1130	37	3.9290	0.0023
Middle temporal gyrus	R	48 –59 4	1556	37	4.3237	0.0016
Fusiform gyrus	L	–46 –70 –10	1234	19	3.8575	0.0025
Fusiform gyrus	R	44 –66 –12	1588	19	4.1743	0.0018
Fusiform gyrus (anterior)	L	–37 –52 –14	517	19	3.7685	0.0027
Inferior occipital gyrus	R	36 –80 –1	1248	18	4.1439	0.0018
Middle occipital gyrus	L	–35 –77 5	422	19	3.5800	0.0035
Middle occipital gyrus	L	–40 –62 7	578	37	3.8498	0.0026

These coordinates represent the center of gravity of the cluster in Talairach space. The t -value is the average value of the cluster, and the p -value the average value for the voxels contained in the cluster. All contrasts have been cluster threshold corrected for multiple comparisons at a level of $p < 0.005$. BA = Brodmann area.

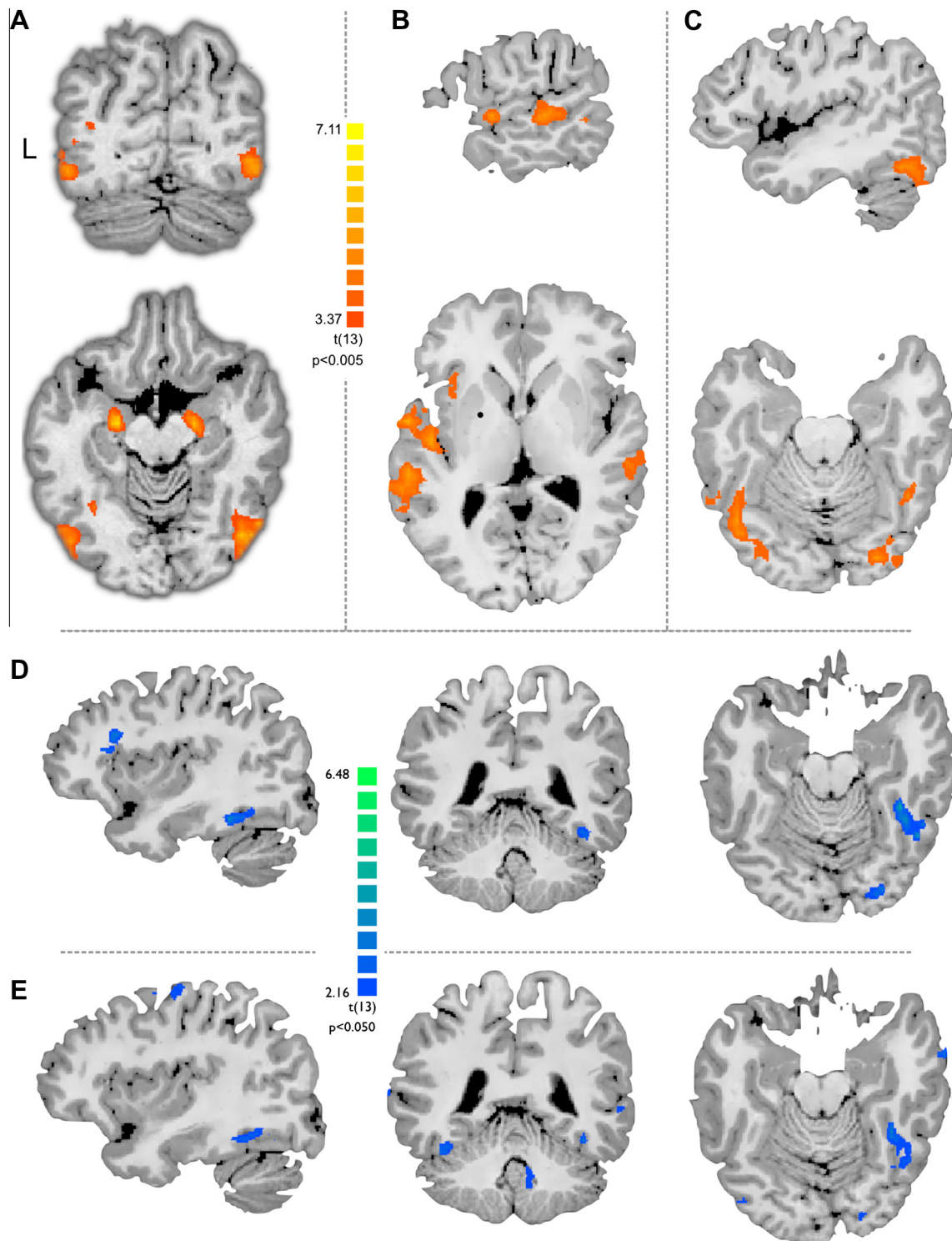


Fig. 1. (A) Univariate analysis. Contrast for affective emotional facial expression against a neutral facial expression giving activation of the amygdala, middle temporal gyrus and fusiform gyrus. (B, C) *t*-Test for instantaneous GCM between EMO and NEU for left and right amygdala seeds revealed connectivity differences in the fusiform gyrus, inferior occipital area and temporal pole. Only the left amygdala showed (bilateral) connectivity with the superior temporal gyrus, IFG and auditory cortex. (D, E) *t*-Test between the directed GCM results of EMO and NEU revealed a connectivity difference in the right fusiform gyrus for both left and right amygdala. The source of influence to both left and right amygdala is lateralized in the right fusiform gyrus/sulcus.

different from a standard correlation value in that the instantaneous correlation is conditioned on the past of the involved time-series. The advantage is that this way

all linear statistical dependence between two time-series is divided into directional (x to y and y to x) and instantaneous correlation.

Seeding regions were defined according to univariate analysis results of the contrast between EMO and NEU conditions. For all seeding regions, a region in the left hemisphere was defined as well as a region in the right hemisphere. The seed regions used were: amygdala, inferior occipital area, and superior temporal gyrus/MTG. For each subject and each region a GCM analysis was performed (FDR corr. $q < 0.05$) and the resulting beta values were used as input for a random-effects (RFX)-GCM over all subjects (FDR corr. $q < 0.05$). Subsequently a paired t -test was performed between the RFX-GCM beta values for EMO and NEU to reveal the effect of emotional affective expression within the neural network.

RESULTS

Memory test

Participants showed equal memory performance for EMO (Hits minus false alarms 74.3%, SD 8.9) and NEU (72.8%, SD 9.1) stimuli. This indicates that both classes of stimuli had been attended during the scanning session.

Univariate statistical analysis

The second level analysis, using the beta values of the first level analysis, revealed greater activation in bilateral amygdala, fusiform gyrus, MTG, and inferior occipital gyrus for emotional vs. neutral animations (Table 1, Fig. 1A). As in both conditions the words were spoken with an appropriate emotional prosody, this contrast could be also thought of as congruent (same emotional valence in the visual and auditory modality) vs. incongruent (visual modality: neutral; auditory modality: emotional). There were no brain areas which showed greater BOLD modulation for neutral animations at the

chosen threshold (cluster threshold corrected for multiple comparisons at a level of $p < 0.005$).

Connectivity analysis

The Instantaneous GCM for the right amygdala (Fig. 2) and left amygdala (not shown) revealed a comparable network encompassing bilateral fusiform gyrus, inferior occipital areas, auditory cortex, superior temporal gyrus, parahippocampal gyrus, medial frontal gyrus, anterior cingulate, putamen and insula (Table 2, Fig. 2). The t -test for Instantaneous GCM between EMO and NEU for left and right amygdala seeds revealed connectivity differences in the respective neural networks. These differences were found in the fusiform gyrus, inferior occipital area and temporal pole. Only the left amygdala showed (bilateral) connectivity with the superior temporal gyrus, IFG and auditory cortex (Table 4, Fig. 1B, 1C).

The Directed GCM for the right amygdala (Fig. 2) and left amygdala (not shown) seeds revealed a network in which both right and left amygdala receive input from the right fusiform gyrus and from bilateral superior temporal gyrus, putamen, IFG, anterior cingulate gyrus, posterior cingulate gyrus, thalamus and anterior temporal pole. In addition, the right amygdala also receives input from the bilateral auditory cortex, cerebellum and early visual areas. Both left and right amygdala show output to bilateral inferior occipital areas, parahippocampal gyrus and caudate (head). Only the left amygdala shows output into the left fusiform gyrus.

A t -test between the Directed GCM results of EMO and NEU revealed a connectivity difference in the right fusiform gyrus for both left and right amygdala. In addition, there was a connectivity difference in the anterior part of bilateral fusiform gyrus and in the right

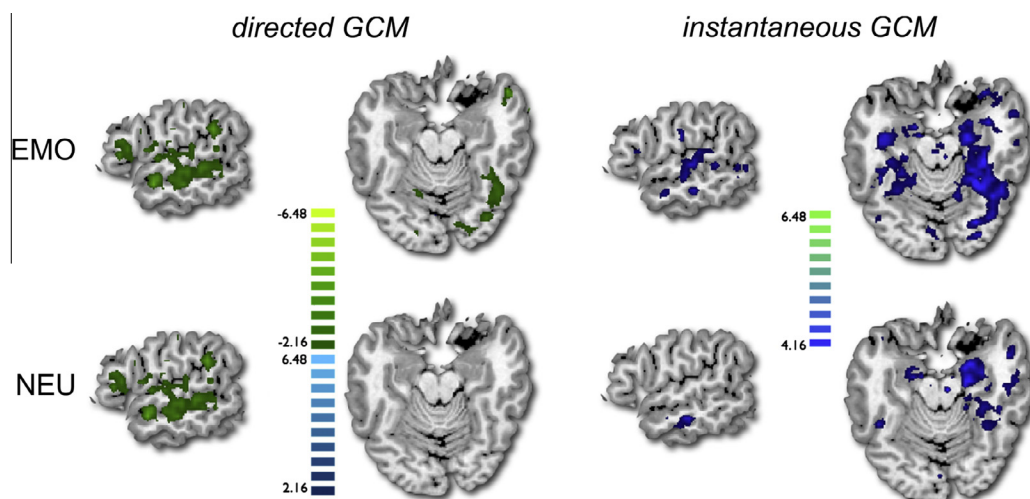


Fig. 2. The directed GCM results for the right amygdala show connectivity with the right fusiform gyrus and superior/middle temporal gyrus. Positive t -values (blue) denote influence from the seeding region to the indicated cluster and vice versa, negative t -values (green) denote influence from the indicated cluster on the seeding region. The Instantaneous GCM for the right amygdala revealed a network encompassing bilateral fusiform gyrus, inferior occipital areas, auditory cortex, anterior temporal pole, medial frontal gyrus, cingulate gyrus and pons. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 2. Seed right amygdala (TAL 18–12–10). Brain areas revealed by instant GCM analysis for emotional (EMO) and neutral (NEU) conditions

Region of activation	Laterality	Coordinates	BA	<i>t</i> Value	<i>p</i> Value
<i>Instant RH amygdala EMO</i>					
Fusiform gyrus	R	29–34–16	20	4.756	0.0005
Fusiform gyrus	R	33–51–16	37	4.821	0.0004
Middle occipital gyrus	R	47–52–6	37	4.887	0.0004
Middle temporal gyrus	R	59–17–12	21	4.522	0.0006
Middle temporal gyrus	R	532–16	21	4.494	0.0006
Superior temporal gyrus	R	57–151	22	4.558	0.0006
Superior temporal gyrus	R	54–209	41	4.426	0.0007
Amygdala	R	25–6–8		5.793	0.0002
Parahippocampal gyrus	R	22–28–3	27	4.691	0.0005
Parahippocampal gyrus	R	8–421	30	4.608	0.0005
Parahippocampal gyrus	R	21–29–7	28	4.706	0.0005
Medial frontal gyrus	R	111442	32	4.589	0.0006
Fusiform gyrus	L	–36–38–16	20	4.497	0.0006
Fusiform gyrus	L	–40–57–11	37	4.988	0.0004
Middle temporal gyrus	L	–48–584	37	4.809	0.0004
Superior temporal gyrus	L	–46–6118	39	4.635	0.0005
Superior temporal gyrus	L	–55–248	41	4.519	0.0006
Superior temporal gyrus	L	–46–102	22	4.803	0.0005
Middle temporal gyrus	L	–53–28–2	21	4.392	0.0007
Middle temporal gyrus	L	–56–8–8	21	4.804	0.0005
Amygdala	L	–23–10–9		4.927	0.0004
Lingual gyrus	L	–12–521	19	4.675	0.0005
Thalamus	L	–12–310		4.821	0.0005
Anterior cingulate	L	–1461	32	4.710	0.0005
Cingulate gyrus	L	–91640	32	4.635	0.0006
<i>Instant RH amygdala NEU</i>					
Fusiform gyrus	R	33–45–16	37	4.615	0.0006
Fusiform gyrus	R	31–36–16	20	4.569	0.0006
Middle temporal gyrus	R	51–15–17	21	4.541	0.0006
Superior temporal gyrus	R	4410–9	38	4.554	0.0006
Parahippocampal gyrus	R	20–13–14	28	6.495	0.0001
Parahippocampal gyrus	R	6–340	30	4.715	0.0005
Fusiform gyrus	L	–40–44–15	37	4.499	0.0006
Middle temporal gyrus	L	–51–542	37	4.526	0.0006
Amygdala	L	–20–10–10		4.753	0.0005
Thalamus	L	–12–313		4.669	0.0005
Anterior cingulate	L	–147–3	32	4.564	0.0006
Parahippocampal gyrus	L	–4–440	30	4.793	0.0005
Middle frontal gyrus	L	–211956	6	4.599	0.0005
Superior temporal gyrus	L	–47–115	22	4.373	0.0007

Clusters were found in the volume data. The Talairach coordinates represent the center of gravity of the cluster. BA stands for the Brodmann area. The *t*-value is the average value for the cluster, and the *p*-value the average value of the voxels contained in the cluster.

hemispheric STS/MTG for the right amygdala seed (Table 2, Fig. 1D, E).

DISCUSSION

We used fMRI in combination with functional connectivity analysis to investigate the integration of emotional facial expression and emotional auditory input. The univariate analysis revealed bilateral activation in the inferior occipital areas, fusiform gyrus and amygdala for emotional vs. neutral stimuli with is in line with earlier studies (Haxby et al., 2000; Adolphs, 2002a,b; Ethofer et al., 2006a). Please note, that we contrasted emotional facial information (positive or negative) paired with emotionally congruent (positive or negative) prosody and emotionally neutral faces paired with

incongruent emotional (positive or negative) prosody, rather than focusing on differences between positively and negatively valence stimuli. While there is evidence for specialization for certain brain areas for positive or negative emotional information (Wager et al., 2003), the emphasis of the current study was on the congruency/incongruency of facial and prosodic information.

Importantly, the fusiform gyrus was more activated for EMO than NEU implicating this structure in the processing of affective facial expressions again compatible with earlier studies (Adolphs, 2002b; de Gelder et al., 2003; Ganel et al., 2005; Vuilleumier, 2005; Ishai, 2008). In addition, the MTG next to the STS showed more activation for EMO compared to NEU stimuli as well. This echoes earlier observations suggesting a role of this region for the integration of

Table 3. Seed right amygdala (TAL 18–12–10). Brain areas revealed by directed GCM analysis for emotional (EMO) and (NEU) conditions

Region of activation	Laterality	Coordinates	BA	<i>t</i> Value	<i>p</i> Value
<i>Directed RH amygdala EMO</i>					
Lingual gyrus	R	16–81–8	18	–2.516	0.028
Cingulate gyrus	R	7–2532	23	–2.547	0.027
Cingulate gyrus	R	122630	32	–2.503	0.029
Middle frontal gyrus	R	473423	46	–2.538	0.027
Inferior frontal gyrus	R	43930	9	–2.639	0.025
Middle temporal gyrus	R	58–21–3	21	–2.642	0.023
Superior temporal gyrus	R	43–44 15	13	–2.542	0.028
Fusiform gyrus	R	38–59–11	37	–2.483	0.298
Putamen	R	30–167		–2.425	0.032
Thalamus	R	11–177		–2.522	0.028
Superior temporal gyrus	R	52–13 11	22	–2.489	0.030
Inferior parietal lobule	R	53–3729	40	–2.614	0.025
Parahippocampal gyrus	R	5–380	30	2.581	0.026
Caudate head	R	2 11 1		2.657	0.024
Parahippocampal gyrus	L	–10–412	30	2.457	0.031
Superior temporal gyrus	L	–45–29 12	41	–2.581	0.026
Superior temporal gyrus	L	–44–51 17	21	–2.397	0.034
Putamen	L	–2378		–2.493	0.029
Anterior cingulate	L	–9445	32	–2.556	0.027
Posterior cingulate	L	–8–65 16	31	–2.671	0.023
Medial frontal gyrus	L	–94624	9	–2.443	0.032
Precuneus	L	–20–7027	31	–2.561	0.027
Cingulate gyrus	L	–4–2734	31	–2.628	0.024
Superior temporal gyrus	L	–49–44 14	22	–2.454	0.031
Inferior frontal gyrus	L	–54527	9	–2.674	0.023
<i>Directed RH amygdala NEU</i>					
Superior temporal gyrus	R	47–319	41	–2.801	0.018
Middle temporal gyrus	R	49–534	37	–2.160	0.025
Superior frontal gyrus	R	434030	9	–2.574	0.026
Inferior parietal lobule	R	57–1923	40	–2.464	0.030
Posterior cingulate	R	10–67 11	30	–2.341	0.036
Cingulate gyrus	R	5–6026	31	–2.357	0.035
Caudate head	R	8–172		–2.469	0.031
Putamen	L	–24–14 10		–2.529	0.028
Transverse temporal gyrus	L	–50–25 11	41	–2.601	0.026
Lingual gyrus	L	–2–73–4	18	–2.401	0.033
Precuneus	L	–9–62 18	31	–2.471	0.030
Superior temporal gyrus	L	–52–210	21	–2.626	0.024
Postcentral gyrus	L	–55–26 17	40	–2.503	0.030
Precentral gyrus	L	–35 11 38	9	–2.472	0.031

Clusters were found in the volume data. The Talairach coordinates represent the center of gravity of the cluster. BA stands for the Brodmann area. The *t*-value is the average value for the cluster, and the *p*-value the average value of the voxels contained in the cluster. Positive *t*-values denote influence from the seeding region to the indicated cluster and vice versa, negative *t*-values denote influence from the indicated cluster on the seeding region.

emotional information from face and voice (Pourtois et al., 2005; Ethofer et al., 2006a,b; Kreifelts et al., 2007, 2009).

Directed Granger causality was used to shed some light on the direction of information flow between the amygdala and the fusiform gyrus. The GCM technique is specifically aimed at extracting the direction of information flow in the brain without prior assumption on that direction (directed GCM), or showing that no such direction can be found (instantaneous GCM). Directed GCM showed a difference in connectivity direction between the right and left hemisphere, from the amygdala to the fusiform gyrus. Bilateral amygdala receives input mainly from the right hemisphere fusiform gyrus and output is directed mainly to the left hemisphere. This difference might explain why some studies report bilateral activation of the fusiform gyrus

with possible right hemispheric dominance (Allison et al., 1994; Pourtois et al., 2005; Kanwisher and Yovel, 2006; Engell and Haxby, 2007) while other studies report mainly or only activation in the right hemisphere (Rossion et al., 2003; Ganel et al., 2005; Vuilleumier and Pourtois, 2007). This difference in activity between both hemispheres might be dependent on the processing route via intermediate task-related areas.

The results are summarized in Fig. 3 with brain areas revealed by our analysis displayed as boxes and information flow as arrows. The brain network is organized into a model taking previous models as a departure point. According to the classical model by (Bruce and Young, 1986) facial expression and facial identity are processed by separate routes. This separation is also a feature of a model proposed by

Table 4. Instantaneous GCM and directed GCM analysis, emotional expression (EMO) > neutral expression (NEU)

Region of activation	Laterality	Coordinates	BA	t Value	p Value
<i>Instantaneous left amygdala EMO > NEU</i>					
Superior temporal gyrus	R	58–122	22	2.581	0.0269
Middle temporal gyrus	R	54–29–4	21	2.383	0.0343
Lingual gyrus	R	13–90–13	18	2.163	0.0306
Lingual gyrus	L	–9–93–9	17	2.161	0.0356
Superior temporal gyrus	L	–483–1	22	2.160	0.0233
Superior temporal gyrus	L	–48–11–1	22	2.734	0.0218
Middle temporal gyrus	L	–55–393	22	2.160	0.0222
<i>Instantaneous right amygdala EMO > NEU</i>					
Fusiform gyrus	L	–41–59–20	37	2.669	0.0237
Fusiform gyrus	L	–40–52–20	37	2.575	0.0274
Lateral occipital gyrus	L	–28–85–14	18	2.429	0.0323
Lingual gyrus	L	–12–83–14	18	2.465	0.0306
Fusiform gyrus	R	26–84–16	18	2.600	0.0267
Inferior occipital gyrus	R	38–82–17	18	2.482	0.0305
Fusiform gyrus	R	41–50–19	37	2.536	0.0280
<i>Directed left amygdala EMO > NEU</i>					
Uncus	L	–296–23	28	2.560	0.0272
Fusiform gyrus	R	22–84–15	37	–2.464	0.0308
Fusiform gyrus	R	38–49–15	21	–2.704	0.0233
Middle temporal gyrus	R	61–28–6	21	–2.489	0.0302
Middle temporal gyrus	R	63–9–6	18	–2.472	0.0314
<i>Directed right amygdala EMO > NEU</i>					
Inferior occipital gyrus	L	–43–81–12	19	–2.591	0.0271
Fusiform gyrus	L	–33–74–10	22	–2.420	0.0329
Middle temporal gyrus	L	–59–384	22	–2.307	0.0397
Superior temporal gyrus	L	–4811–4	37	–2.311	0.0387
Fusiform gyrus	R	43–59–17	37	–2.504	0.0291
Fusiform gyrus	R	21–80–13	19	–2.355	0.0362
Middle temporal gyrus	R	56–34–3		–2.421	0.0323
Middle temporal gyrus	R	62–6–6	21	–2.642	0.0250

These coordinates represent the center of gravity of the cluster in Talairach space. The *t*-value is the average value of the cluster, and the *p*-value the average value for the voxels contained in the cluster. All contrasts have been cluster threshold corrected for multiple comparisons at a level of $p < 0.005$. BA = Brodmann area.

Haxby et al. (2000) who, on the basis of neuroimaging results, posit that the inferior occipital gyri are involved in early perception of facial features. From there, one pathway goes to the STS, which is thought to process changeable aspects of faces such as direction of eye gaze, view angle, emotional expression, and lip movement. Another pathway goes to the lateral fusiform gyrus, which is responsible for processing identity. Our extension of the model also integrates the processing of other information such as non-verbal emotional information. We propose that the dynamic extraction of information from faces and its integration with corresponding auditory information is achieved by the interplay of several different systems: (A) an Input system features components responsible for visual analysis, directing visual attention and auditory analysis (Calder and Young, 2005; Vuilleumier and Pourtois, 2007), (B) a Limbic system hosts components responsible for the extraction of emotional information from the input signal, which is rapidly transmitted to both cortical and sub-cortical areas (Adolphs, 2002b). The amygdala has been implicated as a crossmodal integration site for emotional information (Dolan et al., 2001). In the current instantiation, the model does not distinguish between processing of positive or negative

emotional information. Given the amygdala's preference for negative information, further studies should test the model with regard to the valence of the stimuli. (C) An Integration system is hypothesized to integrate the information from the different systems (Campanella and Belin, 2007; Ethofer et al., 2006b). The STS is the main component of the integration system. Previous studies (e.g., Calvert et al., 2000; Szyck et al., 2008) have used the principle of superadditivity to demonstrate the role of the STS as an integration site. This principle has been criticized (Hocking and Price, 2008) but other findings, most notably the differences observed for congruent and incongruent stimuli (e.g., Szyck et al., 2009) suggest that one of the manifold functions (Hein and Knight, 2008) of the STS is crossmodal integration. (D) Finally, a context system is responsible for further task-related processing (Adolphs, 2002b). The functions of the systems are well documented in the neuroimaging literature and its connectivity pattern, empirically identified in the current experiment, dovetails nicely with other connectivity studies (Ethofer et al., 2006a; Fairhall and Ishai, 2007).

To summarize, Granger causal modeling allowed us to identify a network of brain areas involved in the integration of emotional facial and auditory information

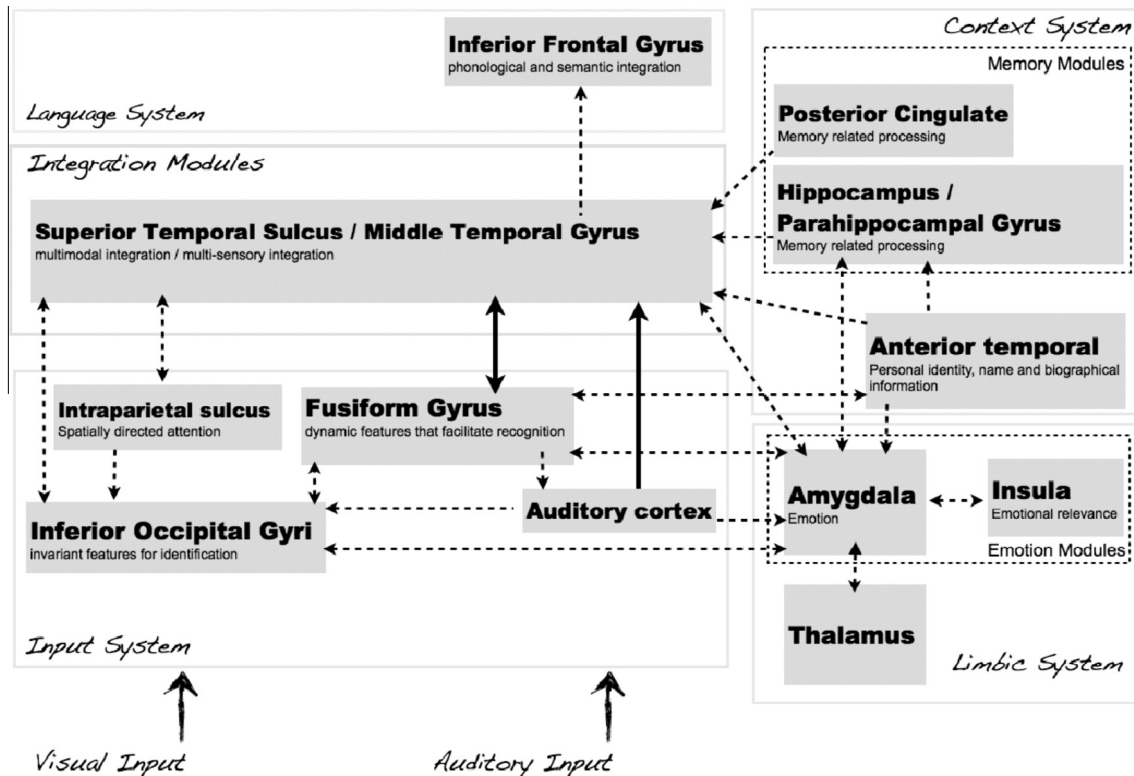


Fig. 3. Summary of the imaging results. Identified brain areas are grouped into several different systems with the information flow between areas denoted by arrows. For explanation, see main text.

and to delineate the information flow between these areas.

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APPENDIX A. SUPPLEMENTARY DATA

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.neuroscience.2013.10.047>.

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