

Neural Correlates of Explicit Social Judgments on Vocal Stimuli

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Functional neuroimaging research on the neural basis of social evaluation has traditionally focused on face perception paradigms. Thus, little is known about the neurobiology of social evaluation processes based on auditory cues, such as voices. To investigate the top-down effects of social trait judgments on voices, hemodynamic responses of 44 healthy participants were measured during social trait (trustworthiness [TR] and attractiveness [AT]), emotional (happiness, HA), and cognitive (age, AG) voice judgments. Relative to HA and AG judgments, TR and AT judgments both engaged the bilateral inferior parietal cortex (IPC; area PGa) and the dorsomedial prefrontal cortex (dmPFC) extending into the perigenual anterior cingulate cortex. This dmPFC activation overlapped with previously reported areas specifically involved in social judgments on 'faces.' Moreover, social trait judgments were expected to share neural correlates with emotional HA and cognitive AG judgments. Comparison of effects pertaining to social, social-emotional, and social-cognitive appraisal processes revealed a dissociation of the left IPC into 3 functional subregions assigned to distinct cytoarchitectonic subdivisions. In total, the dmPFC is proposed to assume a central role in social attribution processes across sensory qualities. In social judgments on voices, IPC activity shifts from rostral processing of more emotional judgment facets to caudal processing of more cognitive judgment facets.

Keywords: fMRI, social cognition, social judgments, temporo-parietal junction, voice evaluation

Introduction

Presumably as adaptive guidance in social interaction, humans automatically engage in social trait estimations of other individuals from the first impression (Bourdieu 1979). In this context, 2 of the most influential and most studied social judgments are those on trustworthiness (TR; Winston et al. 2002; Engell et al. 2007; Baas et al. 2008; Todorov and Engell 2008; Todorov, Baron, et al. 2008; Said et al. 2009) and attractiveness (AT; Bray and O'Doherty 2007; Kim et al. 2007; Cloutier et al. 2008; Chatterjee et al. 2009). TR judgments govern generosity in economic trust games (van't Wout and Sanfey 2008) and the selection of cooperation partners in daily life (Cosmides and Tooby 1992). Similarly important, AT judgments influence human behavior beyond the choice of potential mating partners (Zebrowitz and Montepare 2008): Attractive individuals receive longer eye-contact from infants (Langlois et al. 1991), higher salaries (Frieze et al. 1991), and even lower penalties (Stewart 1980; Langlois et al. 2000).

Besides behavioral studies reporting high intercorrelation of both judgments (Todorov 2008; Todorov, Baron, et al. 2008;

Todorov, Said, et al. 2008), neuroimaging research indicates a largely overlapping neural basis for both types of decisions on others (Bzdok et al. 2011; Bzdok, Langner, et al. 2012; Mende-Siedlecki et al. 2012). Furthermore, TR and AT have been described as "complex social judgments" (Adolphs 2003) involving neural components from multiple functional domains, including affective responses and rational reasoning. For example, trustworthy and attractive faces are consistently shown to recruit brain regions that also respond to basic emotions, such as the amygdala (Bzdok et al. 2011; Mende-Siedlecki et al. 2012). Given that social trait formation is delicately biased by momentary expressions of emotions (Knutson 1996), complex social assessment has been suggested to extend neural systems for emotional processing (Todorov 2008; Todorov, Said, et al. 2008; Oosterhof and Todorov 2009). On the other hand, TR and AT characterize identity traits, which are expected to remain relatively stable over time, prospecting for long-term interaction such as cooperation and mating. In contrast, judgments about basic emotions such as happiness (HA) target more time-variant features of other individuals (Ekman 1992), limiting their social impact to immediate reactions (Izard 2007). Therefore, cognitive systems may modulate emotional information during social judgment formation (Cunningham et al. 2004).

Emotional and cognitive subsystems may, however, not completely explain the neural basis of social trait judgments. To dissociate the emotional and cognitive components from complex social judgments, a recent functional magnetic resonance imaging (fMRI) study in our lab directly contrasted TR and AT judgments with 2 different control conditions, HA and age (AG) judgments, as examples for more emotional and cognitive judgments, respectively (Bzdok, Langner, et al. 2012). Since HA judgments have frequently been used to study the neural correlates of basic emotions (Adolphs et al. 1996; Dolan et al. 1996; Gorno-Tempini et al. 2001; Fusar-Poli et al. 2009; Morelli et al. 2012), they were employed as a control condition for emotional assessment during social trait judgments (Bzdok, Langner, et al. 2012). Conversely, AG judgments have been commonly used as cognitive control conditions against both emotional and social judgments (Habel et al. 2000; Gur et al. 2002; Karafin et al. 2004; Harris and Fiske 2007; Winston et al. 2007; Gunther Moor et al. 2010; Bos et al. 2012), assuming AG discrimination to involve relatively little emotional, but more cognitive features such as memory-related processes (Winston et al. 2007). The results of our previous fMRI study confirmed complex social judgments to share neural patterns with emotion (HA) as well as trait (AG) recognition. Intriguingly, TR and AT judgments showed specifically higher responses than both control conditions in dorsomedial

prefrontal cortex (dmPFC) and inferior frontal gyrus (IFG), possibly due to enhanced integration of other- and self-related knowledge during social judgments (Bzdok, Langner, et al. 2012). That is, previous research on face judgments showed that, well in line with behavioral data, complex social judgments share features with both emotional and cognitive judgments, but also revealed that on top of these commonalities specific neuronal correlates for these complex social trait assessments may be identified. Taken together, the complexity of social trait judgments such as TR and AT has been suggested to contain at least 3 components: Both judgments may involve 1) recognition of emotional states, 2) cognitive trait assessment, and most specifically, 3) integration of self-oriented values and goals. The correlates of social trait judgments could thus be dissociated from its inherent emotional and trait-related processes.

Notably, neuroimaging research including our previous study traditionally focused on face-derived judgments. This is somewhat surprising as voices not only provide information on the sender's affect and identity (Belin et al. 2004), but also on TR (Rockwell et al. 1997; Streeter et al. 1977) and AT (Hughes et al. 2004). Analogously to faces, voice decoding involves distinct neural pathways leading to conceptual processing of affect and identity in transmodal brain areas, such as IFG and posterior cingulate cortex (PCC), respectively (Campanella and Belin 2007; Belin et al. 2011). The roles of these pathways in complex social judgments, for example, TR and AT, on vocal stimuli are yet very poorly understood. The present study, therefore, aimed at the dissection of the neural components of complex social judgments on voices, comparing social trait judgments (TR and AT) with emotional state (HA) and identity trait (AG) judgments on vocal stimuli. The paradigm including its 4 judgment conditions was designed in close analogy to our previous study on social face judgments (Bzdok, Langner, et al. 2012) to increase the comparability of both studies. In total, blood oxygenation level-dependent (BOLD) responses of 44 healthy right-handed adults were scanned rating short everyday sentences recorded from 40 different individuals. Aiming at the isolation of top-down effects driven by the particular judgment task, the presented stimuli were balanced across judgment conditions. Thus, stimulus-driven BOLD effects were selectively partialled out when subtracting any pair of 2 judgment conditions.

Drawing parallels from facial judgments proposes the following hypotheses: Comparing with social judgments on

faces, social judgments on voices also share a neural basis with emotional and trait-related judgments. Candidate regions for such shared processing are the IFG and posterior superior temporal sulcus (pSTS), both associated with judgment tasks on vocal affect (Ethofer et al. 2006; Schirmer and Kotz 2006; Wildgruber et al. 2006). Less is known about the neural basis for auditory trait-related judgments, such as AG. Yet, the PCC, which has been observed higher activated in AG, compared with AT judgments (Winston et al. 2007), has been suggested to integrate identity features on a transmodal level (Campanella and Belin 2007). Moreover, social trait judgments on voices are expected to engage specific brain regions when compared with emotional or trait-related control tasks. They include the dmPFC, a transmodal region, which has been discussed to reflect higher self-related processing during TR and AT judgments. Testing whether the effects during vocal judgments overlap with previous data on facial judgments might further indicate modality-independent underpinnings of social trait judgments.

Materials and Methods

Participants

Forty-four healthy, right-handed adults (21 females, 36.0 ± 11.2 years, range 21–60 years) without any neurological or psychiatric disorder, nor contraindications for fMRI, participated in the study. All participants had normal or corrected-to-normal vision. Written informed consent, approved by the local ethics committee of the School of Medicine of the RWTH Aachen University, was obtained before entering the study.

Stimuli

In total, 40 sentences (2409 ± 356 ms) from 40 native German speaking individuals (20 females, 40.7 ± 14.9 years, range 20–83 years) were recorded, so that each sentence was spoken by a different voice. Sentences contained everyday statements of relatively neutral matter, such as “Entschuldigung, wissen Sie, wie spät es ist?” (“Excuse me, do you know what time it is?”) or “Hallo! Darf ich sie kurz stören?” (“Hello. May I bother you for a moment?”). Moreover, 4 additional sentences, spoken by further different individuals, were recorded to provide a demo set of voices for a training session before the fMRI paradigm. The experiment was run using the Presentation 14.2 software package (Neurobehavioral Systems, Inc., San Francisco, CA, USA). All auditory stimuli were recorded at a sampling rate of 44.1 kHz and presented via headphones.

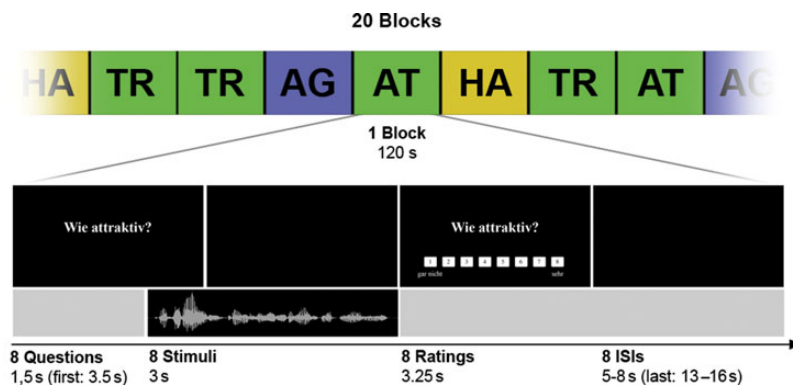


Figure 1. Schematic illustration of the MRI experiment with a timeline for trials of one block. In each trial, participants were asked to rate a voice recording with respect to 1 of the 4 questions: “How trustworthy?” (TR), “How attractive?” (AT), “How happy?” (HA), and “How old?” (AG). ISI, interstimulus interval.

Experimental Paradigm

The experiment consisted of 20 blocks, with 5 blocks per condition, each block including 8 trials, resulting in 160 trials in total (Fig. 1). Importantly, “condition” refers to the judgment the subject had to make and not to different stimulus material. That is, 40 different stimuli were presented once for every judgment condition. Thus, for every condition or judgment type, the same stimulus material was used.

Every trial started with the instruction, which indicated the judgments, participants had to make on the upcoming stimuli. This instruction consisted of one of the following questions (in German): “How trustworthy?,” “How attractive?,” “How happy?,” and “How old?” Within one block, participants rated stimuli regarding solely one judgment category. The instruction of the first trial of every block was displayed for 3.5 s and every subsequent trial of the block was preceded by the same question for 1.5 s. Subsequently, vocal stimuli were presented 0.5 s before the judgment question disappeared, for a maximum of 3 s. After vocal stimulus presentation, stimulus rating was prompted for 3.25 s displaying the initial question together with an 8-point Likert scale, ranging from 1 (“not at all”) to 8 (“very”, e.g. trustworthy). Participants were instructed to judge the voices intuitively and quickly using one of the left and right 4 long fingers. Every block was followed by a short resting baseline from 13 to 16 s and within each block, intervals between trials were randomly jittered, varying from 5 to 8 s. Importantly, we investigated the 4 judgment conditions in separate blocks, but modeled each individual trial individually in an event-related manner. Whereas the block segmentation of trials reduced potential task-switching and sequence effects, the event-related analysis increased specificity by elimination of instruction frames and pauses between trials on a trial-by-trial basis.

In total, 160 trials in 20 blocks were presented to each participant. As one block of 8 trials lasted 2 min, the overall experiment lasted 40 min. Blocks were presented in a pseudorandomized order with each of the 4 judgment conditions represented in 5 blocks (40 trials). Across all blocks, all 40 stimuli were pseudorandomly presented exactly once in every judgment condition. Importantly, using identical stimulus material in all 4 conditions enabled isolation of top-down effects depending on the type of judgment, rather than the actual stimuli. Before the scan, all participants performed a short training session with a demo set of voices to ensure comprehension of the required task.

Behavioral Data Analysis

The behavioral data obtained during the fMRI experiment were analyzed off-line using MATLAB and IBM SPSS 21.0.0. To test for significant differences in reaction times between conditions, a repeated-measures analysis of variance (ANOVA) was computed. Violations of sphericity were Greenhouse–Geisser corrected. Furthermore, correlations between stimulus ratings across different judgment conditions were tested, performing Pearson correlation analyses. All data were confirmed to be normally distributed.

fMRI Image Acquisition

Imaging data were acquired on a 3-T Siemens MRI whole-body system (Siemens Medical Solutions, Erlangen, Germany) with the vendor-supplied 12-channel phased-array head coil. The BOLD signal was measured using a 2-dimensional (2D) echo-planar imaging (EPI) sequence with the following parameters: Gradient-echo EPI pulse, echo time = 30 ms; repetition time = 2200 ms; field of view = $192 \times 3 \times 192$ mm³, $3 \times 3 \times 3$ mm³ within-slice pixel size; flip angle = 90°. Whole-brain coverage was achieved with 36 axial scans with 3.1 mm slice thickness (distance factor = 15%). In total, 1088 volumes were acquired. The initial 4 of these images were dummy scans to allow for longitudinal equilibrium and were discarded before further analysis.

fMRI Image Processing

Using SPM8 (Wellcome Department of Imaging Neuroscience, London, UK; <http://www.fil.ion.ucl.ac.uk/spm>), the EPI images were corrected for head movement by affine registration using a 2-pass procedure, by which images were initially realigned to the first image and subsequently to the mean of the realigned images. After realignment,

the mean EPI image for each subject was spatially normalized to the Montreal Neurological Institute (MNI) single-subject template (Holmes et al. 1998) using the “unified segmentation” approach (Ashburner and Friston 2005). The resulting parameters of a discrete cosine transform, which define the deformation field necessary to move the participant data into the space of the MNI tissue probability maps, were then combined with the deformation field transforming between the latter and the MNI single-subject template. The ensuing deformation was subsequently applied to the individual EPI volumes that were hereby transformed into the MNI single-subject space and resampled at 1.5 mm isotropic voxel size. The normalized images were spatially smoothed using an 8-mm full-width at half-maximum Gaussian kernel to meet the statistical requirements for corrected inference on the general linear model and to compensate for residual macroanatomical variations. Spatial smoothing is also a necessary prerequisite for correcting the statistical inference using Gaussian random field (GRF) theory. Thresholds using the GRF theory to control corrected *P*-values assume that the residual field is a sufficiently smooth lattice approximation of an underlying smooth random field. Only if these requirements are met, the resel count, denoting the kernel that an independent noise field needs to be convolved to yield the same smoothness as the residuals, becomes meaningful.

fMRI Image Analysis

The fMRI data were analyzed using a general linear model as implemented in SPM8. Each experimental condition and its ratings was modeled using the stimulus onset and the time until a response was made convolved with a canonical hemodynamic response function and its first-order temporal derivative. Low-frequency signal drifts were filtered using a cutoff period of 128 s. Parameter estimates were subsequently calculated for each voxel using weighted least squares to provide maximum-likelihood estimators based on the temporal autocorrelation of the data (Kiebel and Holmes 2003).

Besides, the regressors according to the experimental tasks, 2 other regressors were based on the response onset, that is, button presses with the left or right hand to capture motor activity. In particular, the 2 motor regressors were especially introduced into the design to remove the motor-related variance from the fMRI time-series signal. Additionally, we included 6 nuisance regressors as movement parameters to remove artificial motion-related signal changes. For each subject, simple main effects for each experimental condition were computed by applying appropriate baseline contrasts.

The individual first-level contrasts of interest were then fed into a second-level, random-effects ANOVA (factor: condition, blocking factor subject). In the modeling of variance components, we allowed for violations of sphericity by modeling nonindependence across images from the same subject and allowing unequal variances between conditions and subjects as implemented in SPM8. Simple main effects of each task (vs. resting baseline) as well as comparisons between experimental factors were tested by applying appropriate linear contrasts to the ANOVA parameter estimates. Composite main effects (i.e., activations, which were present in each of 2 different conditions) were tested by means of a conjunction analysis using the minimum statistic (Nichols et al. 2005). The resulting SPM(t) and SPM(F) maps were then thresholded at voxel-level $P < 0.001$. Secondly, based on the random field theory, statistical maps were cluster-level corrected (family-wise error (FWE) corrected for multiple comparisons, Worsley et al. 1996) at $P < 0.05$ (cluster-forming threshold at the voxel level: $P < 0.001$).

Anatomical Localization

The anatomical localizations were obtained using the SPM Anatomy Toolbox (Eickhoff et al. 2005, 2007). By means of a maximum probability map, activations were assigned to the most likely cytoarchitectonic area. These maps are based on earlier studies about cytoarchitecture, intersubject variability, and quantitatively defined borders of areas. Please note that not all areas have been cytoarchitectonically mapped, so not all activations could be assigned to a cytoarchitectonic correlate. If no observer-independent 3D delineations were available, anatomical localizations were assigned to Brodmann’s areas (Brodmann 1909) to provide the highest possible level of anatomical information.

Results

Behavioral Results

A repeated-measures ANOVA indicated significant differences in reaction times between conditions (Greenhouse–Geisser corrected: $F_{2,27, 97.6} = 10.43$; $P = 3.7 \times 10^{-5}$). Post hoc tests revealed significantly longer reaction times in the TR condition compared with all other conditions (TR: 1154 ± 398 ms; AT: 1051 ± 351 ms; HA: 1032 ± 367 ms; AG: 998 ± 373 ms; $P < 0.001$ Bonferroni corrected). Reaction times between AT, HA, and AG judgments did not differ significantly from each other (AT – HA: 19 ms, $P = 1.00$; AT – AG: 53 ms, $P = 0.61$; HA – AG: 33 ms, $P = 1.00$), whereas participants took significantly more time for TR judgments (TR – AT: 103 ms, $P = 6.8 \times 10^{-5}$; TR – HA: 122 ms, $P = 2.7 \times 10^{-4}$; TR – AG: 155 ms, $P = 4.8 \times 10^{-4}$).

Correlation analysis revealed positive correlations between ratings of TR, AT, and HA (AT – TR: $r = 0.61$, $P = 2.7 \times 10^{-5}$; TR – HA: $r = 0.53$, $P = 4.6 \times 10^{-4}$; AT – HA: $r = 0.78$, $P < 0.1 \times 10^{-5}$), whereas AG negatively correlated with AT and HA (AG – AT: $r = -0.79$, $P < 0.1 \times 10^{-5}$; AG – HA: $r = -0.57$, $P = 1.2 \times 10^{-4}$). No significant correlation was found between stimulus ratings of AG and TR (AG – TR, $r = -0.10$, $P = 0.55$). These results indicate that stimuli that were estimated to belong to older speakers tended to be rated lower in AT and HA, but not in TR judgments.

The mean number of missed responses of participants per condition did not differ significantly: On average, 0.66 responses were missed in 40 TR judgments, 0.52 in 40 AT judgments, 0.70 in 40 HA judgments, and 0.57 in 40 AG judgments. In other words, only every second participant missed about one response in each category.

To test interrater reliability, Cronbach's alphas were computed across all participant's ratings for each judgment type (α [TR] = 0.90; α [AT] = 0.89; α [HA] = 0.91; α [AG] = 0.82). Although all judgments may contain subjective features, the consistency

of ratings indicates large agreement among participants in all 4 judgment conditions.

Imaging Results

All reported fMRI results were derived from whole-brain analyses, are reported in the MNI space, and survived FWE corrected thresholding on cluster level ($P < 0.05$).

We implemented AG and HA judgments as 2 different control conditions to allow a more precise dissociation of the neural effects underlying explicit social trait judgments. On the one hand, brain regions involved in the judgment of basic emotions were expected to be up-regulated in metabolic activity by explicit HA judgment. On the other hand, regions stimulated by cognitive tasks, which are relatively unrelated to emotional assessment of vocal features, were meant to be specifically enhanced by explicit AG judgment.

First, to delineate brain regions specifically activated during TR and AT judgments, a conjunction was computed among all contrasts comparing their hemodynamic effects (TR and AT) relative to control conditions, that are HA and AG judgments [(TR – HA) \cap (AT – HA) \cap (TR – AG) \cap (AT – AG)]. This conjunction analysis revealed significantly higher responses of the dmPFC (BA 9), extending into the perigenual anterior cingulate cortex (BA 32, BA 24; pACC) (Vogt et al. 2003; Palomero-Gallagher et al. 2009), the left superior frontal gyrus (BA 9; SFG), and bilateral inferior parietal cortex (IPC, areas PGa bilaterally, right PGp and PFm, Caspers et al. 2008) during TR and AT compared with explicit HA or AG judgments (Table 1 and Fig. 2). In a more liberal approach, we only subtracted each one of the control conditions from the effects of TR and AT (see Supplementary Fig. S1). HA judgments were assumed to involve brain regions for basic emotion recognition, but less trait-related elaboration, as expected in TR and AT judgments. Therefore, the conjunction [(TR – HA) \cap (AT – HA)] allowed to remove those neural effects from the activation during social trait judgments,

Table 1.
Main effects of social judgments and shared emotional and cognitive components

Macroanatomical location	<i>k</i>	Cytoarchitectonic area	<i>x</i>	<i>y</i>	<i>z</i>	<i>T</i>
Main effects of social judgments						
[(TR – HA) \cap (AT – HA) \cap (TR – AG) \cap (AT – AG)]						
L dmPFC (extending into right hemisphere)	6638		–4	58	9	7.04
L inferior parietal cortex	1603	IPC PGa	–51	–56	36	6.91
L superior frontal gyrus	486		–22	52	24	4.64
R inferior parietal cortex	370	IPC PGp	45	–60	30	4.35
		IPC PGa	56	–58	36	3.80
		IPC PFm	56	–51	32	3.49
Overlapping effects during social and emotional judgments						
[(TR – AG) \cap (AT – AG) \cap (HA – AG)]						
L inferior parietal cortex	1030	IPC PFm	–57	–54	27	5.91
		IPC PFcm	–52	–44	27	4.76
L inferior frontal gyrus	997	Area 45	–51	32	–14	6.26
			–58	22	8	5.42
L superior frontal gyrus	972		–14	28	54	5.59
L temporal pole	468		–50	8	–38	6.11
R inferior parietal cortex (extending into pSTS)	527	IPC PGa	60	–60	14	4.40
		IPC PFm	63	–50	22	3.84
Overlapping effects during social and cognitive judgments						
[(TR – HA) \cap (AT – HA) \cap (AG – HA)]						
L posterior cingulate cortex (extending into right hemisphere)	960		–8	–51	22	5.72
L inferior parietal cortex	536	IPC PGp	–45	–70	32	4.62
L posterior cingulate cortex (extending into right hemisphere)	535		–4	–36	39	4.49
L superior frontal gyrus	516		–26	24	45	4.75

Notes: MNI coordinates derived from respective cluster peaks (*x*, *y*, and *z*), cluster size (*k*) and *T*-scores (*T*). Locations of functional brain activity are assigned to the most probable brain areas as revealed by the SPM Anatomy Toolbox (Amunts et al. 1999; Eickhoff et al. 2005; Caspers et al. 2006).

TR, trustworthiness; AT, attractiveness; HA, happiness; AG, age judgments.

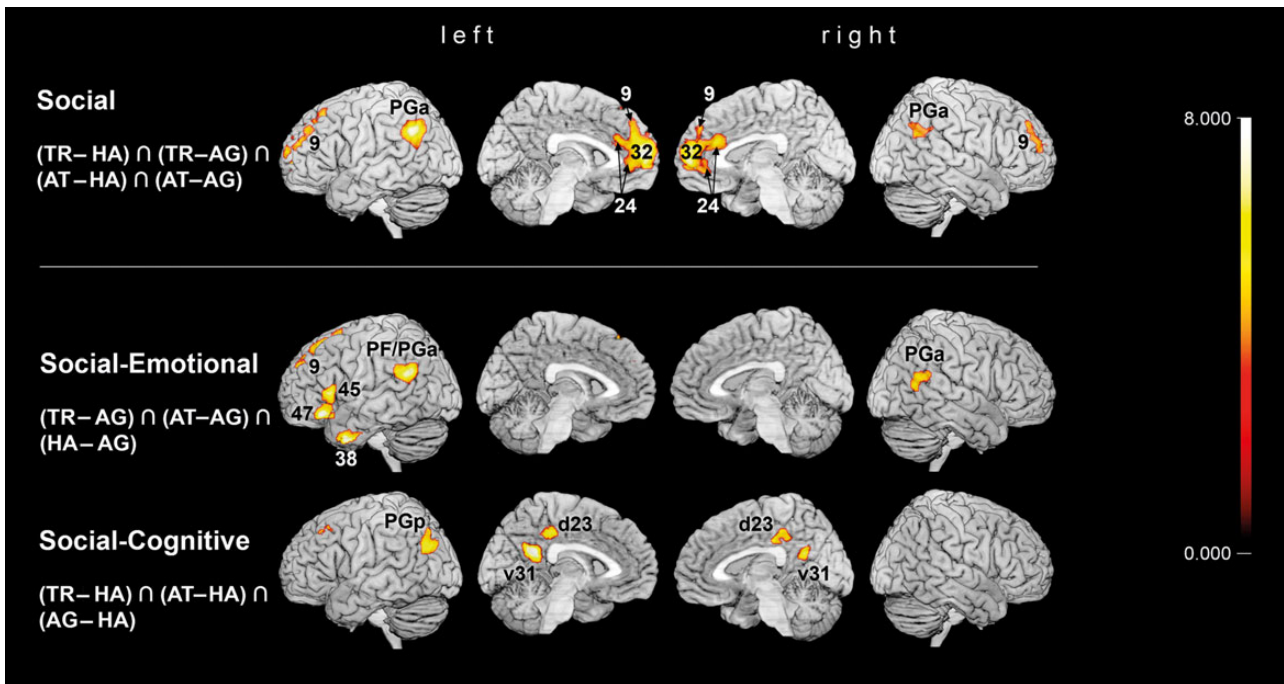


Figure 2. Rendering of brain activations on single-subject MNI templates from top to bottom: Main effects of social judgments TR and AT compared with emotional (HA) and cognitive (AG) judgments; shared activation of social and emotional judgments; shared activation of social and cognitive judgments. As far as possible, clusters are assigned by the SPM Anatomy Toolbox (Amunts et al. 1999; Eickhoff et al. 2005; Caspers et al. 2006). All results are cluster-level corrected at $P < 0.05$ (cluster-forming threshold at voxel level: $P < 0.001$), minimal cluster sizes after cluster-level correction: $[(TR - HA) \cap (AT - HA) \cap (TR - AG) \cap (AT - AG)] = 370$; $[(TR - AG) \cap (AT - AG) \cap (HA - AG)] = 468$; $[(TR - HA) \cap (AT - HA) \cap (AG - HA)] = 516$.

which relate to basic emotion recognition. In contrast, AG judgments have been suggested to involve brain regions for cognitive trait assessment, but less emotion-related features than social trait judgments. Hence, the conjunction $[(TR - AG) \cap (AT - AG)]$ aimed to dissect the neural correlates of TR and AT judgments from trait-related features. These 2 conjunctions allow a more detailed view on the common neural patterns of TR and AT judgments depending on the contrasted control condition.

After opposing social trait judgments to both control conditions, we tested for commonalities between social trait judgments and one control condition compared with the other. Thus, a conjunction of TR, AT, and HA relative to AG judgment effects $[(TR - AG) \cap (AT - AG) \cap (HA - AG)]$ was computed to reveal brain regions, which are more involved in social and emotional judgments than in relatively unaffektive AG judgments. Removing the effects of AG judgments revealed a set of brain regions commonly recruited by TR, AT, and HA judgments, composing left IFG (BA 45, BA 47), left temporal pole (BA 38; TP), left SFG (BA 9), bilateral IPC (bilateral areas PFm, left PFcm, and right PGa), extending into pSTS in the right hemisphere. In contrast, social trait judgments were expected to share neural correlates with AG judgments, corresponding to those more cognitive aspects of these complex judgments that are less involved in emotional state evaluation. Hence, a conjunction of TR, AT, and AG judgments, contrasted to HA judgments $[(TR - HA) \cap (AT - HA) \cap (AG - HA)]$, revealed a set of brain regions consisting of PCC (areas d23, v31; PCC bordering precuneus), left superior frontal sulcus, and left IPC (area PGp) (Table 1 and Fig. 2). Comparing all the 3 conjunctions, revealing correlates of social trait judgments and their relations to each control condition, cytoarchitectonical assignment revealed a functional dissociation of the left IPC from rostral to caudal

areas: Social trait and emotional state judgments, compared with AG judgments elicited higher neural activation in rostral IPC (areas PFm, PFcm, and PGa), whereas caudal IPC (area PGp) was engaged higher during social trait and AG, than HA judgments. Social trait judgments, finally, recruited central IPC area PGa specifically stronger than both control conditions (Fig. 4).

It is important to note that we aimed at the investigation of task-driven features of the judgment process, not primarily implicit, stimulus-driven components. We therefore balanced the stimuli across all 4 conditions, so that bottom-up effects are equally presented in judgment conditions and therefore subtracted out in contrasts. Yet, interactions of top-down and bottom-up effects cannot be fully excluded, since different tasks may lead to varying regulation processes on stimulus-driven effects. Consequently, although purely stimulus-driven bottom-up effects are eliminated in our paradigm, the results may contain task-dependent interaction with stimulus information.

Discussion

This fMRI study examined the neural basis of explicit social judgment on vocal stimuli using sentences frequently occurring in everyday social interaction. Hemodynamic responses during 2 complex social trait judgments, namely TR and AT, were characterized in relation to 2 different control tasks: HA judgments as an example for emotional state assessment and AG judgment as a cognitive control condition.

This approach allowed us to specify the neuroanatomy of social trait judgments (TR and AT) and to allocate its components likewise recruited during HA and AG judgments on voices.

Behavioral Data

As demonstrated for face judgments (Todorov, Said, et al. 2008; Bzdok, Langner, et al. 2012), the ratings on vocal judgments also feature high positive correlations between TR, AT, and HA judgments and negative correlations between AG, AT, as well as HA. The observation of older faces appearing less trustworthy, however, was not reproduced for judgments of voices. Robust correlations between different judgments on faces have prompted the concept that social trait judgments involve emotional (Oosterhof and Todorov 2008) and cognitive neural mechanisms (Cunningham et al. 2004). This hypothesis seems to apply to judgments on voices in a similar manner, as indicated by the behavioral results of the current study.

Stimulus Independent dmPFC in Social Trait Judgments

Comparison of the activation patterns during social trait judgments (TR and AT) with those during basic emotional (HA) and cognitive (AG) ones revealed that both social judgments elicit specific neural activity increases in the left SFG, bilateral

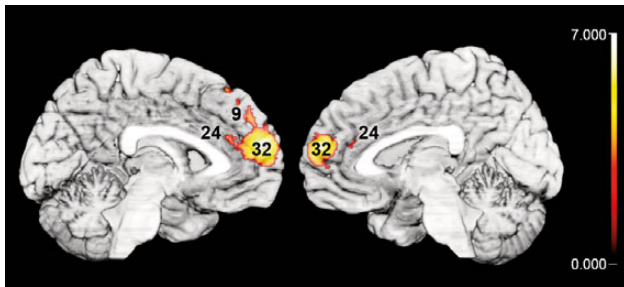


Figure 3. Demonstration of overlap between the main effects of social judgments (TR and AT contrasted to HA and AG judgments) on voices (this study) and on faces (Bzdok, Langner, et al. 2012). Note that congruent increases in brain activation were exclusively located in the dmPFC, as here depicted on medial views of the single-subject MNI template. All results are cluster-level corrected at $P < 0.05$ (cluster-forming threshold at voxel level: $P < 0.001$).

central IPC (PGa), and dmPFC, extending into pACC. Contributions of these brain regions to social trait judgments are, therefore, unlikely to be explained by mere emotional or cognitive processes involved in HA and AG judgments, respectively.

The dmPFC potentially integrates information ranging from reward value to behavioral planning on an abstract level and has been discussed in the domains of action monitoring, mental state inference, and social semantic knowledge about others and self (Amodio and Frith 2006). Among different action identification tasks, enhanced dmPFC activation was, in particular, found when predictions on own and other goals interfered with secondary demanding tasks (Ouden et al. 2005; Spunt and Lieberman 2013). These findings indicate mediation of attentional resources during social reasoning within the dmPFC. Such high-level integration of knowledge about oneself and others may be likely driven by task, independent from the sensory input. Indeed, higher involvement of dmPFC in social trait judgments on vocal stimuli, compared with HA and AG judgments, was well in line with previous results obtained in a very similar setup but using facial stimuli (Bzdok, Langner, et al. 2012). Assuming social trait judgments to specifically recruit dmPFC on a transmodal level, we hypothesized our present results to overlap with the previous data. To test this, we computed a conjunction between the neural correlates during social judgments on faces (earlier study) and on voices (present study). Intriguingly, this analysis revealed a topographical overlap exclusively in the dmPFC (Fig. 3).

These results support the hypothesis of the dmPFC's role in top-down-driven integration of self- and other-related aspects in social cognition (Bzdok, Langner, Schilbach, Engemann, et al. 2013), which may be especially engaged in self-relevant judgments (Seitz et al. 2009). Other than the basic emotional judgment of another's HA or the estimation of another person's AG, TR, and AT judgments imply a long-term prediction for opportunities of social interaction, which may be relevant for the judging individual. Hence, more than HA and

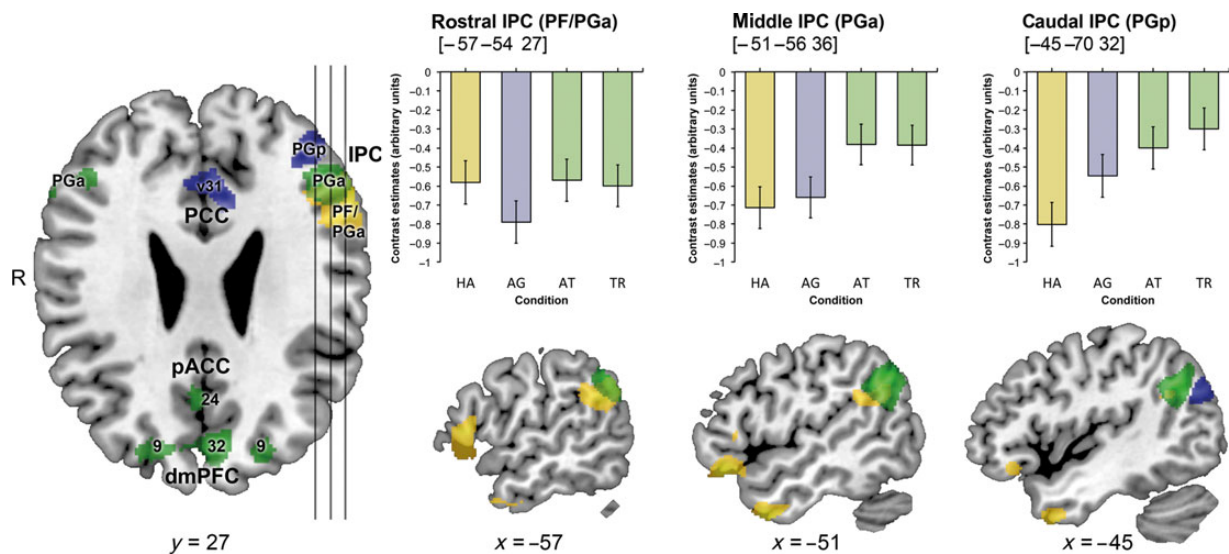


Figure 4. (Left) Axial section showing functionally dissociated areas of the IPC participating in social judgments on voices; green, brain activity in social trait, relative to basic emotion and age judgments; yellow, shared activation of social trait and basic emotion judgments; blue, shared activation of social trait and age judgments. (Right) Sagittal sections through left IPC with relative BOLD changes in all 4 judgment conditions at each contrast's maximum. TR, trustworthiness; AT, attractiveness; HA, happiness judgments; AG, age judgments.

AG judgments, TR and AT judgments require oneself's social knowledge to the perceived, potentially self-relevant characteristics of a voice.

Taken together, the observations of dmPFC engagement in TR and AT judgments on faces as well as voices emphasize its most likely transmodal role in self-relevant integration during social reasoning.

IPC in Social Trait Judgments on Voices

Besides dmPFC, social trait judgments, relative to control conditions, specifically recruited bilateral IPC. Owing to its functional involvement in a broad spectrum of neural processes such as semantics, comprehension, unconstrained cognition, memory retrieval, social cognition, and its role in attentional reallocation (Corbetta et al. 2008; Bzdok, Langner, Schilbach, Jakobs, et al. 2013; Seghier 2013), a specific role of the IPC in mediating integration of bottom-up perceptual and higher conceptual processing has been suggested (Ciarumelli et al. 2008; Seghier 2013). With regard to vocal sentence perception, imaging data on language processing robustly associated IPC activation with phonological, syntactical, and semantic assessment of vocal information (Shalom and Poeppel 2008; Binder et al. 2009; Price 2010). Additionally, lesion studies reported impairment of auditory-verbal memory in patients with left IPC disruption (Warrington and Shallice 1969; Baldo and Dronkers 2006).

Given the left-hemispheric dominance in linguistic processing, it may be tempting to explain the left-lateralized results by the use of sentence stimuli. Although stimuli were identically presented in all judgment conditions to minimize stimulus-driven effects, interactions of stimulus and task effects may involve, for example, sentence processing. However, lateralization has been shown less dependent of stimuli than tasks (Stephan et al. 2007). A previous fMRI study pitted the influence of stimuli and tasks on hemispheric lateralization against each other, similarly using identical stimuli (written words) in different task categories, demonstrating leftward lateralization in a linguistic task and rightward lateralization in a visuospatial task (Stephan et al. 2003). In total, assuming lateralization to be dominated by the task, rather than by stimulus, we emphasize the present left-dominant lateralization to relate to top-down social trait judgment processing on vocally presented sentences.

Indeed, social tasks such as evaluating people (Zysset et al. 2002), uncovering lies (Harada et al. 2009), detecting embarrassment and guilt (Takahashi et al. 2004), and reasoning about other's minds (Lissek et al. 2008) or moral dilemmata (Bzdok, Schilbach, et al. 2012) have frequently reported IPC engagement. Investigating vocal judgments, a recent fMRI study provides evidence for the IPC's role in implicit AT processing on vocal sounds (Bestelmeyer et al. 2012). Stimulus-driven effects depending on the voices' AT were found in the left parietal, temporal, and inferior frontal cortex, but only IPC and IFG responses survived correction for low-level acoustic components of vocal AT. These results suggest that the left IPC is involved in processing highly associative vocal information beyond its discrete linguistic components. Whereas these previous results report the left IPC to respond to attractive voices 'implicitly', the present study, furthermore, identifies the IPC (PGa) to be recruited in 'explicit' judgments on vocal AT extending into TR. The synopsis of present and previous findings, thus, converges on the possible conclusion that central

parts of the IPC (PGa) link social semantic and highly preprocessed perceptual information during voice assessment.

Interestingly, IPC activity was not solely modulated by social trait judgments, but dissociable areas neighboring PGa are likewise engaged in HA or AG judgments relative to the respective other control condition: Social and emotional judgments commonly recruited rostral IPC and IFG more than AG judgments, whereas all trait-related judgments including AG shared higher neural activity than emotional judgments in caudal IPC (area PGp) and PCC (Fig. 4). The functional co-activation of rostral IPC with IFG and caudal IPC with PCC is well in line with earlier histological examinations and diffusion tensor imaging (DTI) describing alterations in IPC cytoarchitecture, receptor, and connectivity features along a rostro-caudal axis (Caspers et al. 2006, 2008, 2011, 2013). Functional and anatomical connectivity studies in humans (Rushworth et al. 2006; Petrides and Pandya 2009; Uddin et al. 2010; Caspers et al. 2011; Mars et al. 2012) and tracing studies in monkeys (Cavada and Goldman-Rakic 1989; Rozzi et al. 2006) agree on strong connectivity of the rostral IPC with the ventrolateral prefrontal cortex and of the caudal IPC with the temporal lobe, PCC, parahippocampal regions, and hippocampus. Given this pattern of IPC connectivity, our results suggest that vocal judgments involve heterogeneous subdivisions of the IPC contributing to distinct features of social trait judgments.

More globally, fMRI experiments from several domains hint at a segregation of the IPC, following a functional gradient from rostral to caudal locations. For example, semantic representations of concrete sensorimotor knowledge are identified more rostrally in the IPC than those of abstract concepts (Binder et al. 2009). In keeping with a higher level of conceptuality towards caudal IPC, linguistic studies found rostro-caudal trends from phonological to semantic discrimination (Shalom and Poeppel 2008; Sharp et al. 2010). Recent results from the domain of social cognition indicate the rostral IPC to be more engaged in judgments about the present state and biological motion, whereas the caudal IPC is more activated in future prospection and moral judgments (Andrews-Hanna et al. 2010; Bahnmann et al. 2010). Taken together, these findings point to a shifting recruitment from rostral to caudal IPC regions in tasks requiring concrete to abstract processing, respectively.

The present study extends the evidence for functional IPC heterotopy to social trait judgments on voices, relating affect-oriented functions to anterior IPC and rational trait-oriented functions to posterior IPC regions. In the following paragraphs, we offer an interpretation how IPC subdivisions may variably contribute to explicit categorization of voices.

Common Neural Correlates in Social Trait and Emotional State Judgments on Voices

Explicit assessment of TR, AT, and HA, relative to AG, congruently recruited a set of areas, comprising the left IFG, anterior TP, SFG, rostral IPC (assigned to PFm and PFcm), and right rostral IPC (PGa and PFm), extending into the pSTS, which thus indicate the functional basis for emotion assessment inherently engaged during social trait judgments on vocal stimuli.

Rostrally, the IPC has extensive connections to the IFG and sensorimotor cortex, as indicated by in vivo DTI tractography in humans (Makris et al. 2005; Rushworth et al. 2006; Caspers et al. 2011), possibly explaining its functional relation to action

imitation (Decety et al. 2002), judgments of biological motion (Bahemann et al. 2010), and semantic motor-sequence knowledge (Binder et al. 2009). Such processing of motor sequences in rostral IPC and pSTS includes recognition of socially and emotionally meaningful patterns, such as intentional body movement (Saxe et al. 2004; Blake and Shiffrar 2007), facial mimics, and gaze (Haxby et al. 2000; Nummenmaa and Calder 2009) as well as prosody (speech melody) (Wildgruber et al. 2004, 2005). Specifically, emotional prosody is regarded as an essential feature to convey emotions by voice (Belin et al. 2011). To meet an explicit judgment on a voice's affect, current models for emotional prosody processing propose the right pSTS to receive preprocessed acoustic information, which is subsequently fed into the bilateral IFG (Ethofer et al. 2006; Schirmer and Kotz 2006; Wildgruber et al. 2006). Interestingly, the current study revealed higher right pSTS and left IFG activation not only in emotional state, but also social trait judgments on voices, compared with AG judgments. This observation suggests that TR and AT judgments on voices implicitly recruit neural systems associated with emotional prosody processing. Given the high correlation between social and emotional judgments in the behavioral data, it is not surprising that these judgments might be based on common features such as affective prosody appraisal.

However, explicit social and emotional judgment tasks might share more common processes than only the analysis of prosody. First, discrimination tasks of emotional connotation especially recruited a left-lateralized set of brain regions including IFG, rostral IPC, SFG and anterior TP (Ethofer et al. 2006; Beaucousin et al. 2007), concordant with the present results. Although not explicitly requested in judgments on 'voices,' language may have been similarly screened for affective content in complex social and basic emotional judgments, more than in AG judgments. Secondly, higher response in rostral IPC hints at enhanced attention toward the speaker's intentions during TR, AT, and HA judgments. Specifically, the right rostral IPC has been reported to encode other's intentions and to integrate those during social judgment formation (Saxe and Kanwisher 2003; Young and Saxe 2008; Saxe 2010). Correspondingly, social trait and emotional state judgments engaged right rostral IPC higher than the assessment of a physical characteristic (AG).

Taken together, the present findings reveal shared neural mechanisms underlying social trait and emotional state judgments on voices, possibly interpreting relatively short vocal sequences such as prosody and connotation in their social and emotional meaning.

Common Neural Correlates in Social and Rational Trait Judgments on Voices

TR, AT, and AG, relative to HA judgments, concomitantly recruited the left caudal IPC (PGp) and 2 regions in the PCC bordering the precuneus (Margulies et al. 2009), which thus compose a potential functional basis for the categorization of relatively unaffactive, trait-related features in vocal judgments.

Possibly homolog areas in monkeys are not only strongly interconnected, but both, caudal IPC (PGp) and PCC, share strong connectivity to hippocampal and parahippocampal regions as indicated by axonal tracing studies (Goldman-Rakic et al. 1984, Goldman-Rakic et al. 1988; Suzuki and Amaral 1994; Kobayashi and Amaral 2003; Kondo et al. 2005). In humans,

these connections were also described functionally and structurally using resting-state functional connectivity and DTI (Uddin et al. 2010). Functional implications of PGp and PCC include highly abstract, cognitively challenging social processes such as theory of mind, future prospection, navigation, and autobiographical memory (Buckner et al. 2008; Spreng et al. 2009). Moreover, recent fMRI investigations on first impression judgment revealed that PCC activity predicts the extent of positive and negative evaluation (Schiller et al. 2009), especially when judgments are based on verbal information (Kuzmanovic et al. 2012).

Comparing the present results with the meta-analyses of Spreng et al. (2009), we observed striking proximity to 2 PCC regions, consistently engaged in autobiographical memory tasks. Psychological models suggest that autobiographic memory is essential for identity schemes that are consistent over time (Wilson and Ross 2003), and that identity schemes provide a basis to find consistent analogies in one's environment (Bar 2007). Indeed, the present results indicate an up-regulation of PCC and caudal IPC (PGp) in judgments of TR, AT, and AG. Importantly, all 3 of these judgments differ from HA judgments in their consistency over time. In particular, HA, as a basic emotion, resembles an inconsistent state, while the other 3 person characteristics are regarded as enduring traits (Scherer 2005; Izard 2009).

With respect to trait judgments of voices, we consider activity increase in the caudal IPC (PGp) and PCC to reflect memory-informed judgment formation relating stable trait schemes to vocal information.

Conclusion

We investigated the neural basis underlying explicit social trait judgments on voice records of everyday statements. The observed convergence of brain regions recruited during social trait judgments on voices in the present study, and on faces in previous studies, indicates a central, most likely transmodal role of the dmPFC in complex social attribution processes across judgment modalities and sensory qualities. Furthermore, we characterized the functional heterogeneity of the left IPC in social evaluation tasks on voices, suggesting selective recruitment of the IPC along a rostro-caudal functional axis mediating affective processes more rostrally and cognitive trait-oriented features more caudally.

Supplementary Material

Supplementary material can be found at: <http://www.cercor.oxfordjournals.org/>.

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Notes

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