Imaging first impressions: Distinct neural processing of verbal and nonverbal social information

Q1 Bojana Kuzmanovic [a,b,*], Gary Bente [c], D. Yves von Cramon [d], Leonhard Schilbach [d,a], Marc Tittgemeyer [c], Kai Vogeley [a,e]

[a] Department of Psychiatry and Psychotherapy, University Hospital Cologne, Germany
[b] Institute of Neurosciences and Medicine — Ethics in the Neurosciences (INM-8), Research Center Juelich, Germany
[c] Department of Psychology, University of Cologne, Germany
[d] Max-Planck Institute for Neurological Research, Cologne, Germany
[e] Institute of Neurosciences and Medicine — Cognitive Neurology (INM-3), Research Center Juelich, Germany

ARTICLE INFO

ABSTRACT

First impressions profoundly influence our attitudes and behavior toward others. However, little is known about whether and to what degree the cognitive processes that underlie impression formation depend on the domain of the available information about the target person. To investigate the neural bases of the influence of verbal as compared to nonverbal information on interpersonal judgments, we identified brain regions where the BOLD signal parametrically increased with increasing strength of evaluation based on either short text vignettes or mimic and gestural behavior. While for verbal stimuli the increasing strength of subjective evaluation was correlated with increased neural activation of precuneus and posterior cingulate cortex (PC/PCC), a similar effect was observed for nonverbal stimuli in the amygdala. These findings support the assumption that qualitatively different cognitive operations underlie person evaluation depending upon the stimulus domain: while the processing of nonverbal person information may be more strongly associated with affective processing as indexed by recruitment of the amygdala, verbal person information engaged the PC/PCC that has been related to social inferential processing.

© 2012 Published by Elsevier Inc.

Introduction

In our everyday life we are ready to make fast and spontaneous judgments about other persons (Uleman et al., 2008), which are determined by our very subjective evaluation of the available information about the target person (Schiller et al., 2009). Furthermore, first impressions are mostly not restricted to inferences about enduring dispositions, e.g., that someone is intelligent because he passed a math test, but also encompass an evaluative component due to the assignment of a rather positive or negative value to someone's individual characteristics. Importantly, the outcome of such an evaluation crucially determines our expectations and behavior toward social others (Delgado et al., 2005; Uleman et al., 2008).

However, little is known about whether the cognitive processes mediating the evaluation of another person differ depending upon the domain of available information. While the traditional person judgment research has relied on verbal stimuli such as action description or trait adjectives, short excerpts of nonverbal behavior have been demonstrated to be equally effective in evoking differentiated assessments (Ambady et al., 2000; Kuzmanovic et al., 2011). But although ratings of other persons may lead to similar outputs across different domains of information, this does not allow for inferences regarding the degree of similarity of underlying cognitive processes. However, comparing the neural correlates of impression formation that relies on verbal and nonverbal person information, respectively, could be used as an index for such conclusions. Thus, the present study explores putative differences in the neural signature of the evaluative component of impression formation dependent upon whether the underlying relevant social information was presented verbally or nonverbally. Given the far-reaching consequences of impression formation within social interactions, elucidating possible domain-specific differences in the related neural processing would extend the understanding of interpersonal behavior and might have significant implications for social decisions.

Theoretical considerations suggest divergent processing streams across domains by stating that language is digitally defined by an explicit semantic code with a complex logical syntax, while the interpretation of analog nonverbal signals appears to be more uncertain as multiple cues may occur simultaneously and extend over time, and are known to have greater impact on the affective, relational level of communication (Kraemer, 2008; Watzlawick et al., 1967). Supporting these assumptions, a recent neuroimaging study indeed

Q2 * Corresponding author at: Department of Psychiatry and Psychotherapy, University Hospital Cologne, Germany. Fax: +49 221 478 87702.
E-mail address: bojana.k@gmx.net (B. Kuzmanovic).

has demonstrated domain-specific neural systems involved when drawing inferences about social targets' affective states: while verbal information processing was associated with the mental state attribution system including the dorsomedial prefrontal cortex (dmPFC), precuneus (PC), temporopolar and temporoparietal regions, the non-verbal information processing related to the right inferior frontoparietal network corresponding to the putative human mirror neuron system, bilateral amygdala, right superior temporal sulcus (STS) and fusiform gyrus (FFG) (Zaki et al., 2010). Direct comparisons between verbal and nonverbal stimuli though cannot identify specific differences in social cognition because of additionally present basic differences in sensory and cognitive processing across domains.

In the specific context of interpersonal judgments, little is known about the neural processing of dynamic nonverbal behavior. However, studies using still neutral faces have provided consistent evidence for the amygdala being crucially involved in their evaluation with respect to judgments of trustworthiness and valence (Todorov, 2008; Todorov and Engell, 2008; Winston et al., 2002). Although being generally associated with salience detection, and with assigning an emotional value to external cues, the response of the amygdala appears to be particularly sensitive for faces that convey significant social cues (Hariri et al., 2002; Sergerie et al., 2008). In contrast, the processing of verbal person information in the context of interpersonal judgments has been consistently associated with the dmPFC (Harris et al., 2005; Mitchell et al., 2002, 2005; Ochsner et al., 2005; Sugiura et al., 2004; Zysset et al., 2002). While this is in concordance with its central role in mental state attribution and person perception (Amodio and Frith, 2006), it has recently been demonstrated that the dmPFC is not specifically involved in evaluative processes of impression formation (Schiller et al., 2009). Instead, evaluation of others has been shown to differentially engage the amygdala and the posterior cingulate cortex (PCC), which were activated stronger by stimuli that guided subsequent judgments (Schiller et al., 2009). Additionally, these regions also exhibited increases in the BOLD signal with increasing strength of the evaluative judgment (Schiller et al., 2009). The study by Schiller and colleagues, however, failed to investigate putative stimulus domain-specific differences as they used simultaneously both verbal and non-verbal stimuli. Our study was conducted to directly address this aspect: Specifically, we were interested in exploring differences in neural processing of verbal and nonverbal social information, which evokes increasing strengths of evaluative person judgment.

Using functional magnetic resonance imaging (fMRI), we employed an experimental paradigm containing verbal (V) and nonverbal (NV) stimuli of different valences (positive, negative, and neutral). Participants were instructed to rate target persons along a global positive–negative scale based on either a) a short video clip showing an animated virtual character displaying dynamic expressive nonverbal behavior; or b) short verbal action description. Additionally, the arousal of all stimuli was assessed after scanning in order to control for this dimension of person perception. We aimed to identify brain regions whose activity correlated with the 'strength' of subsequent evaluations of social others based either on verbal or nonverbal information (operationalized as a difference from 0 on the rating scale, i.e., including both positive and negative judgments). Notably, we based this analysis on individual responses in order to take into account that the same piece of information can have different meanings or values for different persons. We expected that brain regions, which are involved in the evaluation of others, would increase their activation with increasingly pronounced impressions. By focusing on the parametric modulation of the neural activity by the 'strength of evaluation' (SoE), this paradigm allows to compare different domains, in spite of basic sensory and cognitive stimulus-specific processing differences. The SoE-effect was computed separately for each domain, so that across all events the basic stimulus characteristics were identical and differences related only to the degree to which they, in fact, influenced the subsequent evaluation of the target person.

Methods

Subjects

18 right-handed participants with no reported history of neurological or psychiatric illness were included in the study (9 males, mean age = 24.7, age range 21–29 years). All participants gave informed consent and were naïve with respect to the experimental task and the purpose of the study. The study was approved by the local ethics committee of the University Hospital Cologne.

Stimuli

Positive and negative verbal and nonverbal stimuli were created as reported in detail in Kuzmanovic et al. (2011). Verbal stimuli (V) consisted of sentences describing a social action suitable to induce an impression of a female target person (e.g., "She told the secrets of a colleague to the others." vs. "She did not tell the secrets of a colleague to the others."; see Fig. 1B). Nonverbal stimuli (NV) consisted of dynamic video clips of 3 s duration with an animated female virtual character displaying impression-evoking nonverbal signals. While using the same virtual character for all nonverbal stimuli, the following expressive features were systematically varied: Gaze direction (direct vs. averted gaze), facial expression (smile vs. angry face), body movements (forward vs. backward lean), and head movements (lateral vs. backward flexion) (see Fig. 1A). The purpose of the strict control of the target person's physical appearance was to ensure that both verbal and nonverbal stimuli conveyed individuated social information related to idiosyncratic behavior, which is not reducible to more superficial cues like face morphology or hair color. In addition, neutral verbal (non-social action descriptions: e.g., "She opened the drawer of her desktop.") and nonverbal stimuli (non-expressive facial and body movements) were created in order to enable the comparison between impression-valent and impression-neutral stimuli. In each domain (V, NV), the three valence categories, i.e., negative (−), neutral (0) and positive (+), were matched for complexity. Verbal stimuli did not differ with regard to syntactic complexity as all sentences had a simple structure without any subordinate clauses and the same mean number of words (ANOVA of mean number of words per sentence for −, 0, +, $F(2,33) = .04$, $p = .96$). Furthermore, semantic complexity was also comparable across the valence conditions as there were no differences in the word frequency according to the German vocabulary project of the University of Leipzig (http://wortschatz.uni-leipzig.de/; ANOVA of mean word frequency per sentence for −, 0, +, $F(2,33) = .27$, $p = .76$). Finally, neutral, positive and negative nonverbal stimuli had the same quantity of movement as measured by the mean of frame-to-frame pixel change per stimulus (ANOVA, $F(2,33) = .40$, $p = .67$).

The stimuli were pretested in an independent sample (n = 14) with regard to ratings of valence (−3 = very negative to 3 = very positive) and arousal (−3 = not arousing to 3 = very arousing) resulting in mean ratings shown in Table 1. Paired t-tests revealed that positive verbal and nonverbal and negative verbal and nonverbal stimuli did not significantly differ regarding valence or arousal ratings ($p > .05$ for all comparisons). However, although neutral verbal and nonverbal stimuli were comparable concerning the valence ratings ($p > .05$), they differed with regard to arousal ratings ($t(13) = −2.85$, $p = .01$) with neutral verbal stimuli being rated as less arousing than neutral nonverbal stimuli.

Procedure

Stimulus presentation and response recording were performed by the software package Presentation (version 13.1; Neurobehavioral Systems, Inc). Stimuli were projected onto a screen (Optostim, 32-inch, resolution 1280×800) at the end of the magnet bore that
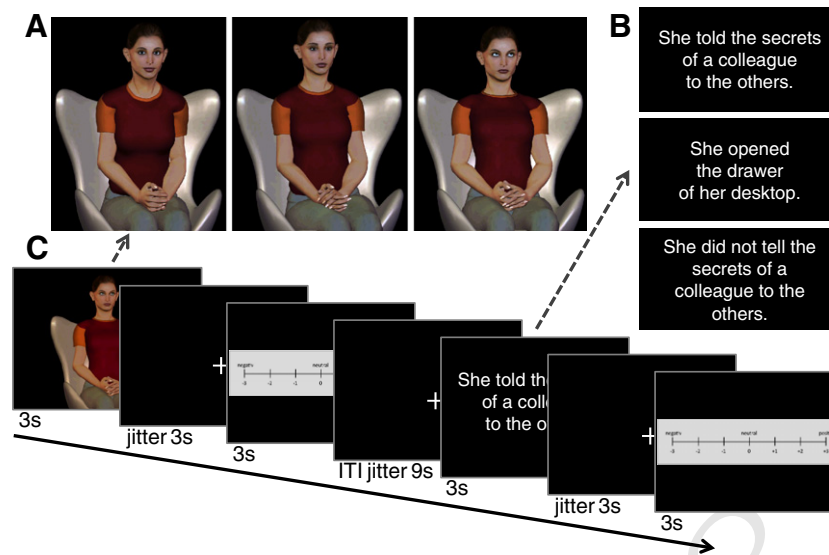
Fig. 1. Examples of verbal and nonverbal stimuli and the experimental procedure of the evaluative impression formation task. A) Example frames from positive, neutral and negative nonverbal video stimuli. B) Example sentences of positive, neutral and negative verbal stimuli. Originally, the sentences were on German, but are translated into English for illustration purposes. C) An example of two subsequent experimental trials: verbal and nonverbal stimuli with differing valences were presented in a randomized order and rated by participants on a 7-point global evaluation rating scale.

participants viewed via a mirror mounted to the head coil. Responses were assessed using a MR-compatible response device (Current Design).

Participants were instructed to judge female job applicants as positive or negative on a 7-point rating scale (−3 = very negative; −2 = negative; −1 = rather negative; 0 = neutral; 1 = rather positive; 2 = positive; 3 = very positive) based on either verbal or nonverbal information. A 7-point scale was used in order to enable participants to give neutral ratings as well. Verbal information was said to provide descriptions of the applicant's behavior toward colleagues at the prior workplace. Nonverbal information was said to be a "thin slice" of the applicant's behavior toward colleagues at the prior workplace. Participants were further instructed to treat the social referent across trials as different target persons. In other words, they were instructed to form a new impression on every trial independently of previously observed person information. It was explained that the nonverbal cues were overlayed on the same virtual character in order to control for effects of physical appearance on impression formation. An experimental trial consisted of a 3000 ms stimulus presentation (either V or NV) followed by a rating scale lasting for 3000 ms. Participants received a visual feedback about their button presses and could correct given responses if necessary until the end of the rating scale slide. Furthermore, each trial entailed two randomly jittered intervals with a fixation cross: one between each stimulus presentation and the following rating scale in order to enable a separate analysis of the person evaluation and the response (average duration 3000 ms, jittering between 1875 ms and 4125 ms) and the other between single trials to increase condition-specific BOLD signal discriminability (Serences, 2004) (average duration 9000 ms, jittering between 7875 ms and 10,125 ms). Taken together, an average trial lasted for 15,000 ms (see Fig. 1C). In total, the task consisted of 72 trials (36 stimuli for each of the two domains)

that were presented in a randomized order within two sessions of 9 min duration each. In one session button presses were performed with the right and in the other session with the left hand, this sequence being randomized across participants. After scanning, participants underwent an additional task, in which they rated all stimuli on a 7-point rating scale measuring arousal.

fMRI acquisition

Functional and structural MRI images were acquired on a Siemens Magnetom Trio 3T whole-body scanner with a Tx/Rx birdcage coil. For the fMRI scans we used a T2*-weighted gradient echo planar imaging (EPI) sequence with the following imaging parameters: TR = 2200 ms, TE = 30 ms, FoV = 210, 33 oblique (maximal 30°) axial slices, and slice thickness = 3.0 mm. Two sessions of 301 images were acquired, preceded by 3 additional images allowing for T1 magnetic saturation effects that were discarded prior to further image processing. For the structural images we used high-resolution T1-weighted modified driven equilibrium Fourier transform sequence with the following parameters: TR = 1930 ms, TE = 5.8 ms, FoV = 256, 128 sagittal slices, and slice thickness = 1.25 mm.

fMRI preprocessing and analysis

Images were preprocessed and analyzed using MATLAB 7.1 (The MathWorks Inc) and SPM8 (The Wellcome Trust Center for Neuroimaging) as follows. After the EPI images were corrected for head movements using realignment and unwarping, the mean EPI image of each participant was computed and coregistered to the corresponding T1 image. The T1 image was then used to obtain normalization parameters for each participant to the Montreal Neurological Institute (MNI) reference space using the unified segmentation function in SPM8. The ensuing deformation was subsequently applied to the individual EPI volumes, the T1 image and the segmented T1 images with a writing resolution of 8 mm³. The normalized EPI images were spatially smoothed using an 8 mm FWHM Gaussian kernel to meet the statistical requirements of further analysis and to compensate for macroanatomical variations across participants.

The data were analyzed using a General Linear Model as implemented in SPM8. The following specifications apply to all conducted analyses. Conditions were modeled using a boxcar reference vector

Table 1
Descriptive statistics of the stimuli: Means and standard deviations of valence and arousal ratings from the pretest.

		−	0	+
Valence	V	−1.88 (.34)	.08 (.16)	2.03 (.27)
	NV	−2.08 (.63)	−.09 (.54)	1.76 (.32)
Arousal	V	1.45 (.98)	−1.66 (1.01)	.04 (1.23)
	NV	.96 (.86)	−.61 (.92)	.32 (.60)

convolved with the canonical hemodynamic response function and its time derivative. The analyses were explicitly masked with a normalized within-brain mask of each subject derived by the segmentation of individual T1-images. Stimulus events were defined by the onsets and durations of corresponding stimulus presentations. Response events were modeled as a separate regressor, with onsets and durations according to the time the rating scale was present. If present, events with missing responses were modeled separately. Low-frequency signal drifts were filtered using a cutoff of 128 s. Following the first-level analyses, single subject contrasts were fed into the group analysis using a flexible factorial ANOVA (factors: condition and subject), employing a random-effects model. On the group level, differences between conditions and significant deviations from zero were assessed by linear contrasts on the second-level parameter estimates thresholded at $p < .05$ at the voxel level, FWE-corrected for multiple comparisons ($p_{FWE-corr} < .05$) and with a minimal cluster size of 30 voxels. Exceptionally, when reporting results from the analysis including both evaluation strength and arousal as parametric modulators a more liberal threshold of $p < .001$ at the voxel level, uncorrected for multiple comparisons ($p_{uncorr} < .001$) was applied as this analysis specifically served to confirm the significant effect of evaluation strength. Results were superimposed on the mean normalized T1-group image.

Three different statistical analyses were conducted. The first analysis focused on the SoE-effect by including both categorical and parametric neural responses to the stimuli into the model: (i) the categorical, general processing of verbal and nonverbal person information, irrespective of its impact on subsequent evaluation (V and NV); and (ii) the parametric modulation of general processing by SoE (SoE-V and SoE-NV, defined as a difference from 0 on a 7-point rating scale: 0, 1, 2 or 3). For illustration purposes only, i.e., in order to provide plots for the better characterization of activation patterns across different SoE levels for significant brain regions, we also employed a categorical analysis, in which V and NV events with different absolute rating values were modeled as separate regressors. Here, eight events of interest were included in the analysis: V0, V1, V2, V3 and NV0, NV1, NV2, NV3 (see plots in Fig. 2A).

Q3

The second analysis aimed to demonstrate that differences in arousal ratings cannot explain the results of the parametric modulation. Here, the first analysis was repeated but with two linear parametric modulation factors: (i) first the arousal rating for each stimulus; and (ii) second the absolute valence rating for each stimulus. At the group level we again computed the SoE-V and SoE-NV contrasts, masked with the results from the main analysis. Because the second parametric modulation can only account for unique variance, which is not already accounted for by the first parametric modulation, this allows for ruling out the influence of the arousal of the stimuli on the impression strength effect.

The third analysis finally aimed to demonstrate that the SoE-effect was similar for positive and negative person information and included six events of interest: V−, V0, V+ and NV−, NV0, NV+. At the group level, valent, i.e. positively and negatively judged events (Val) were compared against neutrally rated events, separately for the verbal (Val-V) and nonverbal (Val-NV) domains (applied contrasts: 1 −2 1).

Results

The first analysis revealed distinct modulations of the general neural response by SoE for verbal and nonverbal stimuli, respectively. When judgments were based on nonverbal information, there was a linear signal increase in the bilateral amygdala with increasing SoE (see Fig. 2A and Table 2, SoE-NV). In contrast, when relying on verbal social information, increasing SoE correlated positively with the signal change in the left PC at the border to PCC (PC/PCC), the bilateral cuneus and cerebellum (see Fig. 2A and Table 2, SoE-V). These effects could mainly be replicated also in a direct comparison of SoE-V and SoE-NV, thereby resembling the plots in Fig. 2A. The contrast SoE-NV > SoE-V revealed a greater increase in the right hippocampus ($x = 32$, $y = −10$, $z = −16$, $T = 5.84$, $p_{FWE-corr} = .002$, cluster size = 48 voxels) and the right amygdala ($x = 24$, $y = 0$, $z = −20$, $T = 5.39$, $p_{FWE-corr} = .009$, cluster size = 48 voxels, same cluster as the hippocampus). Conversely, the contrast SoE-V > SoE-NV revealed a greater increase in the right PC/PCC ($x = 14$, $y = −60$, $z = 34$, $T = 4.97$, $p_{FWE-corr} = .039$, cluster size = 4 voxels) and the right cerebellum ($x = 10$, $y = −50$, $z = −20$, $T = 5.31$, $p_{FWE-corr} = .012$, cluster size = 12 voxels). However, the left amygdala and the bilateral cuneus did not exhibit a significantly different increase with increasing SoE across the two domains. Furthermore, contrasts targeting general responses to verbal and nonverbal stimuli irrespective of SoE revealed more widely distributed patterns of activation (V > NV, NV > V and conjunction between V and NV, V∩NV, see Fig. 3A and Table 3). Categorical comparison of verbal versus nonverbal stimuli revealed a network including the left STS, bilateral inferior parietal lobule (IPL), bilateral temporal pole, left PC/PCC, left dmPFC, left inferior frontal gyrus (IFG), left inferior temporal gyrus and left middle occipital gyrus. The opposite comparison of nonverbal versus verbal stimuli demonstrated involvement of the bilateral middle temporal gyrus, bilateral FFG, the right posterior STS extending into the IPL, the right middle frontal gyrus extending into the IFG, bilateral superior occipital gyrus and cuneus and the right thalamus. Finally, regions commonly activated by both verbal and nonverbal stimuli included the left FFG, bilateral calcarine sulci and inferior occipital gyri, the SMA, the left IPL, the bilateral anterior insula, the superior PC, the bilateral thalamus and the left IFG.
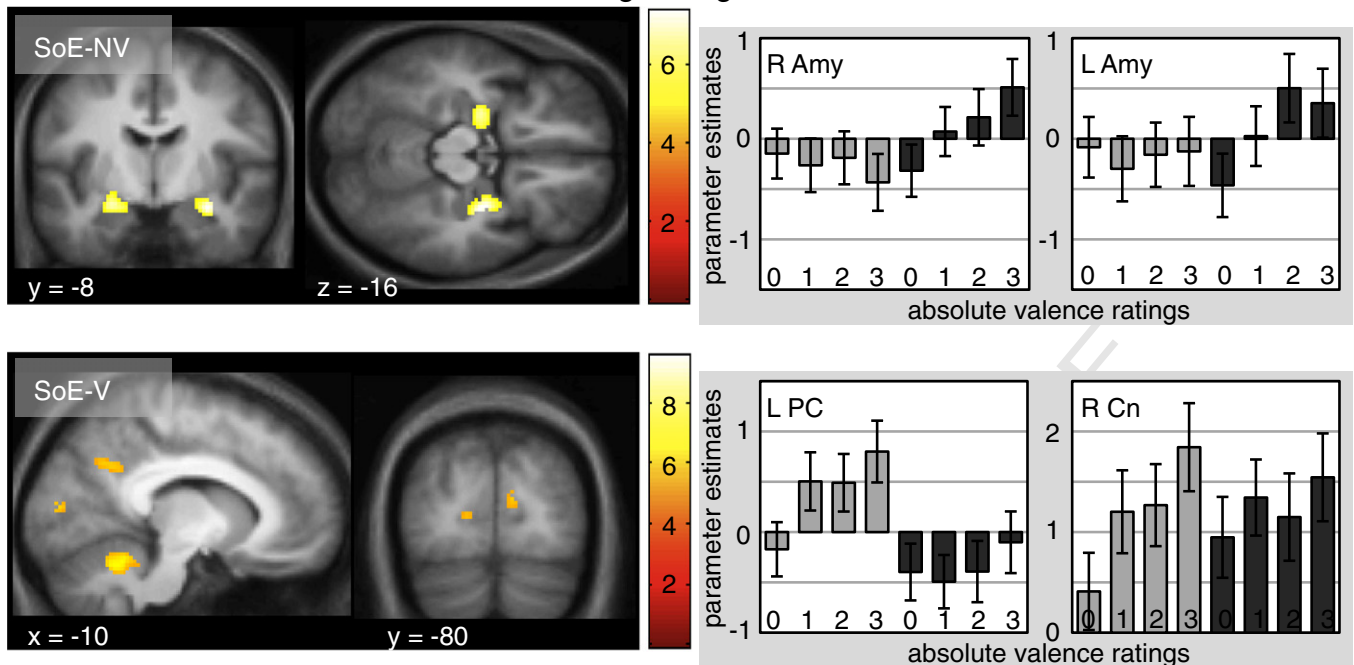
The second analysis included both arousal ratings and absolute valence ratings as parametric modulators in order to control for the effect of stimulus arousal. This analysis replicated the former SoE-effects by showing increasing BOLD signal in the bilateral amygdala with increasing SoE for the nonverbal domain ($x = −22$, $y = −10$, $z = −8$, $T = 4.95$, $p_{uncorr} < .001$, cluster size = 284 voxels and $x = 32$, $y = −12$, $z = −16$, $T = 4.50$, $p_{uncorr} < .001$, cluster size = 125 voxels). Similarly, the equivalent contrast for verbal stimuli revealed the precuneus ($x = −10$, $y = −64$, $z = 36$, $T = 3.76$, $p_{uncorr} < .001$, cluster size = 15 voxels), the cerebellum ($x = 6$, $y = −44$, $z = −24$, $T = 4.99$, $p_{uncorr} < .001$, cluster size = 549 voxels) and the cuneus ($x = 12$, $y = −78$, $z = 12$, $T = 4.50$, $p_{uncorr} < .001$, cluster size = 445 voxels). Thus, as the effects of the second parametric modulation in a model reveal only variance that had not been explained by the first parametric modulation, we can rule out that the effect of the increasing SoE could be explained by differences in stimulus-related arousal ratings.

Finally, the third analysis confirmed that the effect of increasing SoE does not reflect the influence of valence per se because the effect of valent versus neutral ratings was similar for both positive and negative social judgments. By comparing positive and negative against neutral judgments, we fully replicated the results from the first analysis (see Fig. 2B and Table 2, Val-V and Val-NV). In addition, direct comparisons between negative and positive verbal judgments (V− vs. V+ and V+ vs. V−) revealed no significant results within the whole brain, or when inclusively masked with SoE-V, even at a more liberal threshold ($p_{uncorr} < .001$). Similarly, comparing negative and positive nonverbal judgments (NV− vs. NV+ and NV+ vs. NV−) revealed no differences when inclusively masked with SoE-NV, even at a more liberal threshold ($p_{uncorr} < .001$). The comparison between negative and positive nonverbal stimuli within the whole brain, i.e. without masking, however, revealed a significantly stronger activation of the right superior temporal gyrus ($x = 42$, $y = −30$, $z = 12$, $T = 5.77$, $p_{FWE-corr} = .001$, cluster size = 143 voxels) while no significant whole brain effect was found for the opposite contrast (NV+ vs. NV−), even at a more liberal threshold ($p_{uncorr} < .001$).
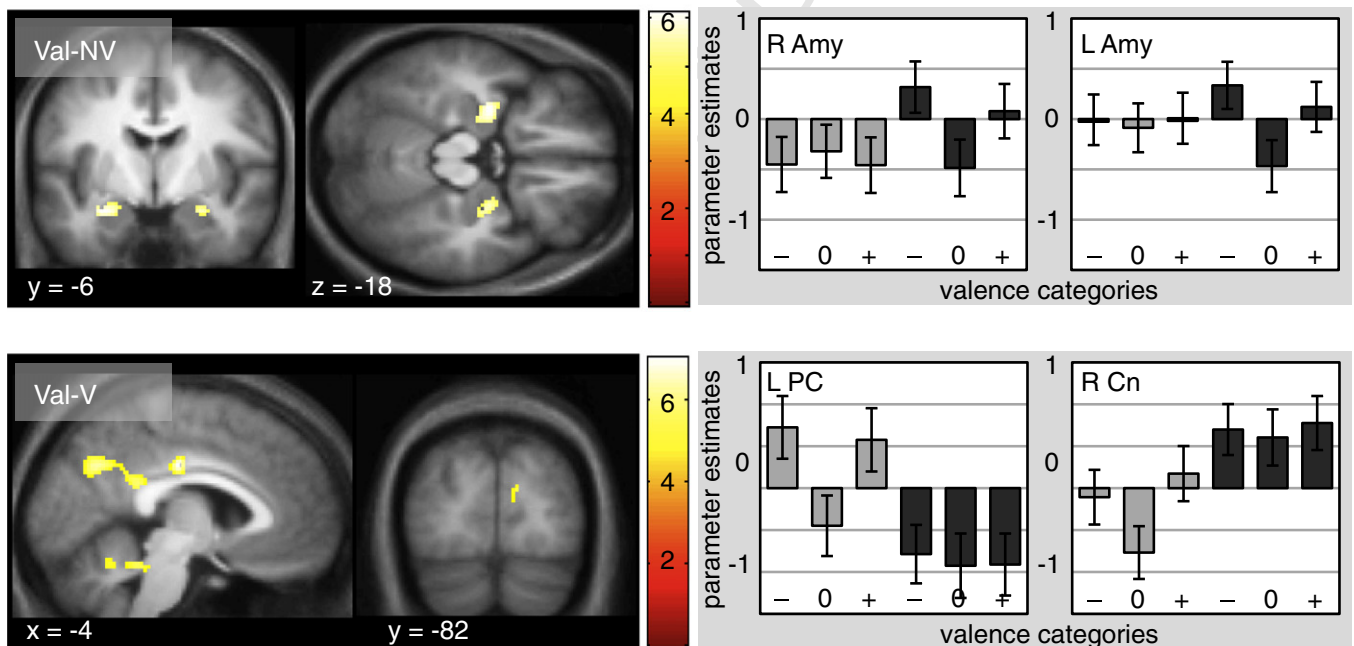
Discussion

The results of the present study show that neural regions specifically associated with increasing SoE during impression formation

Fig. 2. Brain regions responsive to the outcome of subjective evaluative impressions based on a verbal or a nonverbal person information: A) Areas correlating with the increasing absolute valence ratings as a measure of the strength of evaluation (SoE), based on nonverbal (SoE-NV) and verbal (SoE-V) stimuli. Plots are derived by a supplementary analysis modeling events with different absolute ratings (0, 1, 2 or 3) as separate regressors; and B) Areas activating stronger during valent than neutral evaluations (Val), separately for nonverbal (Val-NV) and verbal (Val-V) stimuli, demonstrating a similar involvement for both positive and negative ratings.

differ depending upon the stimulus domain, i.e. between verbal and nonverbal stimuli. These effects were detectible for both positive and negative evaluations and even after controlling for subjectively rated arousal of the stimuli. Although pretests showed that verbal and nonverbal stimuli evoked comparable person evaluations at the behavioral level, increasing evaluation strength was associated with the bilateral amygdala for nonverbal stimuli and with the PC/PCC, bilateral cuneus and cerebellum for verbal stimuli. Hence, this finding indicates an involvement of qualitatively different cognitive processes during the evaluation of other persons dependent upon the stimulus domain.

Known to be a centerpiece of the affective system of the brain, the amygdala has been associated with diverse aspects of affective

Table 2

MNI coordinates of brain regions revealed by the parametric effect of increasing absolute evaluation ratings as a measure of the strength of evaluation (SoE) based on verbal (SoE-V) and nonverbal (SoE-NV) stimuli, and by the comparison between valent and neutral evaluation ratings based on verbal (Val-V) and nonverbal (Val-NV) stimuli.

Region	Cluster size (vox)	BA	Side	x	y	z	t
SoE-V							
Cerebellum	1018	–	R	10	−54	−20	9.54
			L	−6	−54	−22	7.22
PC/PCC	59	31	L	−12	−56	32	6.10
Cuneus	57	17/18	R	12	−76	14	5.67
	53	17	L	−8	−88	10	5.74
SoE-NV							
Amygdala	126	–	R	30	−8	−16	7.36
	110	–	L	−24	−8	−14	6.58
Val-V							
PCC	468	23	L	−10	−52	30	6.40
PC		31	L	−4	−66	34	6.13
Cerebellum	246	–	R	4	−46	−20	5.57
		–	L	−6	−40	−22	5.45
Middle cingulate gyrus	74	23	L	−4	−20	34	6.99
Lingual gyrus	55	17	R	12	−70	0	5.37
Cuneus	46	18	R	12	−82	20	5.35
Val-NV							
Amygdala	132	–	L	−30	−6	−18	6.12
	40	–	R	26	−6	−18	5.52

Reported are results that were significant at the voxel-level threshold $p < .05$, FWE-corrected for multiple comparisons, with a cluster size greater than 30 voxels; x, y, z, MNI coordinates of local maxima; BA, Brodmann area; PC, precuneus; PCC, posterior cingulate cortex; one voxel $= 8 \text{ mm}^3$.

processing and learning (Zald, 2003). Providing further empirical support for its recruitment during the evaluation of other persons, our results also imply two more specific aspects: i) the amygdala was sensitive to changes in evaluation intensities, irrespective of valence; and ii) this response pattern was specific for nonverbal social information.

In concordance with the first point, the idea that the amygdala correlates with affective response intensities in a broad sense has recently received considerable empirical support. Overcoming the traditional conception that the amygdala is associated with negative valence only, neuroimaging studies (Anders et al., 2008; Sander and Scheich, 2001), as well as a quantitative meta-analysis (Sergerie et al., 2008) have demonstrated its recruitment for the processing of positive stimuli as well. Specifically regarding face evaluation, recent studies have shown that both highly trustworthy as well as highly untrustworthy faces activated the amygdala yielding a nonlinear, U-shaped response pattern (Said et al., 2009; Todorov et al., 2008). Similarly, the amygdala was engaged during judgments of absolute valences of emotional faces (Gerber et al., 2008). Furthermore, neuroimaging studies focusing specifically on interpersonal judgments have demonstrated that both positive and negative judgments recruit the amygdala when evaluating famous people (Cunningham et al., 2004, 2008) or when forming evaluative impressions of social others (Schiller et al., 2009). In the same line, the present study revealed that the more the nonverbal behavior displayed by the target person induced a pronounced impression, indexed by a greater SoE, the higher was the BOLD signal in the amygdala. Thus, our findings provide further support for the concept that the amygdala is especially sensitive to varying intensities of salient social information, irrespective of valence (Sander et al., 2003).

The second aspect with regard to the involvement of the amygdala in our study is that its increasing response with increasing SoE was specific for nonverbal stimuli. This result extends the findings by Schiller et al. (2009) by highlighting a closer association of the differential response in the amygdala with nonverbal social information in the context of increasingly extreme interpersonal evaluation. Taking into account its extensive projections to the occipital cortex, the amygdala is well positioned to modulate visual processing based on affective significance of the perceived input (Phelps and LeDoux, 2005; Vuilleumier and Pourtois, 2007). Consistently, converging evidence indicates its modulatory role in visual information processing, but not in recall and auditory induction methods of emotional responses (Phan et al., 2002). Furthermore, support for the specific sensitivity of the amygdala to nonverbal social cues has been provided by impairments in evaluating trustworthiness based on nonverbal, but not on verbal information in patients with amygdala lesions (Adolphs et al., 1998). Moreover, the recruitment of the amygdala for processing nonverbal stimuli has been shown to occur relatively independent of attentional resources or awareness, i.e., implicitly and automatically (Engell et al., 2007; Phelps and LeDoux, 2005; Phelps et al., 2000; Todorov and Engell, 2008; Winston et al., 2002). Although the essential role of the amygdala in the production of the social behavior has been questioned in prior studies on non-human primates, its role in detection of and reaction to especially threatening and hence significant stimuli
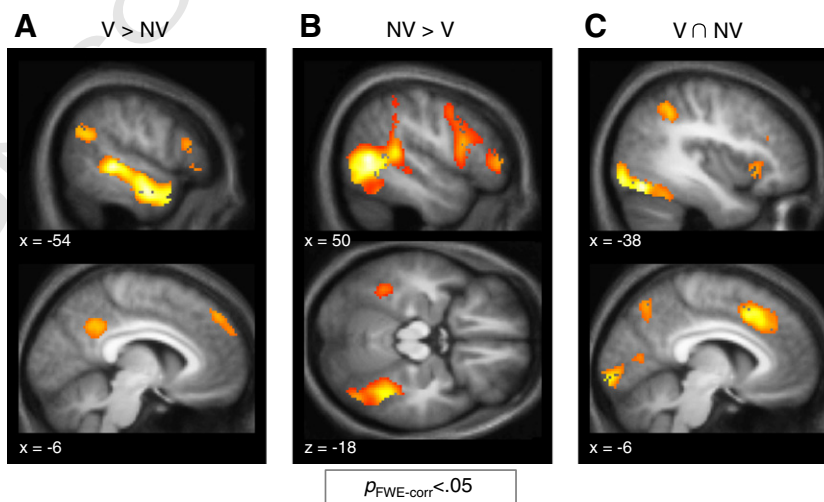

A V > NV	B NV > V	C V ∩ NV
x = -54	x = 50	x = -38
x = -6	z = -18	x = -6

$p_{\text{FWE-corr}} < .05$

Fig. 3. Neuroimaging results relating to the general processing of verbal (V) and nonverbal (NV) person information, irrespective of subsequent ratings. A) Brain regions involved stronger in processing of verbal than nonverbal person information; B) Brain regions involved stronger in processing of nonverbal than verbal person information; C) Brain regions involved in processing of both verbal and nonverbal person information revealed by a conjunction.

Table 3

MNI coordinates of brain regions associated with the general processing of verbal (V) and nonverbal (NV) person information.

Region	Cluster size (vox)	BA	Side	x	y	z	T
V > NV							
Anterior STS	2001	21	L	−58	−6	−20	12.41
Posterior STS		22	L	−54	−36	0	11.66
Temporal pole		38	L	−48	16	−28	9.96
Angular gyrus	815	39	L	−44	−56	24	11.54
Middle occipital gyrus	377	18	L	−18	−90	−6	11.42
PC/PCC	298	31	L	−6	−52	36	7.00
dmPFC	235	9	L	−10	48	40	9.39
Middle frontal gyrus	190	6	L	−42	6	52	6.60
Middle temporal gyrus	148	21	R	58	4	−28	7.43
Temporal pole		21	R	56	10	−30	7.01
Inferior frontal gyrus	121	47	L	−50	30	−8	6.66
Inferior frontal gyrus	78	45	L	−52	24	18	6.26
		44	L	−52	16	28	4.93
Inferior temporal gyrus	67	37	L	−42	−62	−8	7.39
Angular gyrus	37	39	R	60	−58	26	7.10
NV > V							
Middle temporal gyrus, V5/MT+	3897	37	R	50	−62	6	17.06
Fusiform gyrus		37	R	42	−48	−18	12.26
Posterior STS		42	R	50	−40	12	11.87
Supramarginal gyrus		48	R	58	−38	26	10.63
Middle frontal gyrus	1770	10	R	46	42	4	11.04
Inferior frontal gyrus		44	R	48	14	20	9.78
Inferior frontal gyrus		45	R	44	32	16	7.94
Superior occipital gyrus	1404	17	L	−8	−98	12	17.61
Cuneus		18	R	10	−92	22	15.09
Middle temporal gyrus, V5/MT+	575	37	L	−48	−70	8	10.94
Fusiform gyrus	148	37	L	−40	−48	−18	7.42
Thalamus	76	–	R	18	−30	2	6.75
NV ∩ V							
Fusiform gyrus	3387	19	L	−40	−70	−16	12.80
Calcarine sulcus		17	R	16	−96	−6	12.33
		17	L	−6	−98	−6	8.50
Inferior occipital gyrus		19	R	34	−90	−12	12.11
		19	L	−38	−86	−10	10.55
SMA	666	6	L	−6	16	44	9.72
Inferior parietal lobule	382	7	L	−38	−48	44	7.36
Superior parietal lobule		7	L	−30	−60	46	5.45
Anterior insula	371	48	L	−30	20	−4	7.98
Precuneus	191	31	L	−6	−68	50	6.39
Inferior frontal gyrus	174	45	L	−50	30	28	7.63
Anterior insula	111	48	R	42	26	−8	6.05
Thalamus	68	–	L	−10	−12	6	5.54
Middle frontal gyrus	51	9	R	46	36	32	6.77
Thalamus	50	–	R	12	−8	4	6.11

Reported are results that were significant at the voxel-level threshold $p<.05$, FWE-corrected for multiple comparisons, with a cluster size greater than 30 voxels; x, y, z, MNI coordinates of local maxima; BA, Brodmann area; STS, superior temporal sulcus; PC, precuneus; PCC, posterior cingulate cortex; dmPFC, dorsomedial prefrontal cortex; SMA, supplementary motor area; one voxel = 8 mm³.

within a social context has not been disproven (Amaral, 2003; Amaral et al., 2003). Given that understanding information conveyed by conspecifics' nonverbal signals occurs early in phylogenetic and ontogenetic development and plays a special role in adaptive social behavior, our findings may reflect an evolutionary shaped recruitment of the amygdala in the rapid detection and decoding of biologically and socially relevant information (Phelps and LeDoux, 2005; Sergerie et al., 2008).

Interestingly, the presentation of verbal and of neutral nonverbal stimuli was accompanied by deactivations in the amygdala, especially in the right hemisphere (see Fig. 2). Such right amygdala deactivations have been demonstrated already early on, by comparing active and passive conditions of different experiments, i.e. conditions where stimulus presentations were paired with demanding tasks versus with no task (Schulman et al., 1997). Moreover, those experiments that involved verbal processing tended to reveal larger deactivations in the right amygdala (Schulman et al., 1997). General task-induced deactivations are in accord with research demonstrating cognitive regulation of affective processing (Ochsner et al., 2002, 2004). Here, it has been shown that active cognitive computations were able to down-regulate affective processing and thereby decrease amygdala activity. Referring to neutral nonverbal stimuli in our study, the activity in the amygdala associated with detection of salient stimuli was possibly decreased simply because of the non-affective quality. Verbal stimuli, in contrast, may have induced a greater amount of high-level cognitive processing leading to a decreased activity of the amygdala as previously supposed by Freeman et al. (2010) for interpersonal judgments based on informative verbal stimuli. Additionally, paralleling patterns of activations have been demonstrated with other-race facial stimuli that increased the activation of the amygdala, while the perception of more neutral own-race facial stimuli resulted in slight deactivations (Lieberman et al., 2005). Furthermore, matching the race of the target face verbally and not via facial, i.e. nonverbal stimuli resulted in amygdala deactivations for both races (Lieberman et al., 2005).

On the other hand, our study highlights that when basing social judgments on verbal information, the BOLD signal increased in the PC/PCC, bilateral cuneus and cerebellum with increasing SoE. Thus, we replicated the findings by Schiller et al. (2009), who showed a specific involvement of the PCC in the evaluative component of impression formation and its parametric scaling with the SoE. Beyond this general functional characterization, we were able to demonstrate that the PC/PCC and its parametric activity changes are specifically associated with the processing of verbal stimuli. Consequently, our findings provide evidence for functional dissociations of 'social brain' regions based on the stimulus domain.

A similar dissociation has been demonstrated by a stronger involvement of the PCC in the processing of interpersonal judgments based on informative verbal material, while the amygdala was recruited when verbal stimuli were not informative and the judgment was reduced to an additionally presented face of the target person (Freeman et al., 2010). Our study extends these findings because it focuses specifically on the evaluative component of impression formation by making use of event-related subjective ratings instead of comparing two categories of person judgment irrespective of the subsequent outcome. Furthermore, due to the manipulation of both verbal and nonverbal stimuli in one experimental design, more valid conclusions about the influence and processing of the two domains can be derived from our study. Finally, in the present study both verbal and nonverbal information was individuated, i.e. related to idiosyncratic attributes and qualities of the target person indicated by social action descriptions and dynamic nonverbal communicative signals, respectively. Because nonverbal cues were displayed by the same virtual character, the content of social category knowledge extractable from the physical appearance such as gender, age, and race was identical across all nonverbal stimuli and could not serve as a basis for "superficial" decisions. This procedure implicates that not simply the degree of individuation but also the domain of social information determines the involvement of differential brain regions in evaluation of social others.

In general, the neurofunctional characterization of PCC has been more diverse than that of the amygdala. Social cognitive neuroscience research has assigned an important role to the PC/PCC in social inference including mentalizing, intention inference and impression formation (Lieberman, 2010) and in the interaction between episodic memory and the processing of emotionally salient words (Maddock, 1999; Maddock et al., 2003). Also, associations with the strength of evaluative judgments have been demonstrated by using verbal but not nonverbal stimuli (Maddock et al., 2003; Posner et al., 2009). At the same time, this region is characterized by its involvement in controlled, i.e., resource-limited processing in social cognitive tasks (Lieberman, 2010) and thus may also be associated with relatively deliberate processing. Thus, on a more speculative level, by revealing

the association of PC/PCC with the verbal and of the amygdala with the nonverbal domain, we provide indirect evidence for hypotheses made by dual-process theories of social judgments (Evans, 2008; Lieberman et al., 2002). Here, it has been suggested that the two domains evoke automatic and controlled cognitive operations to different degrees that are associated with closely interacting but distinguishable neural substrates.

The cuneus comprising primary and secondary visual areas and the cerebellum were also differentially recruited by increasing evaluation strength based on verbal stimuli. The involvement of the visual cortex may be explained by the increased mental imagery of behaviors described in the more influential verbal stimuli (Lambert et al., 2002), possibly due to a higher selective attention toward a more diagnostic information (Kastner and Ungerleider, 2000). Similarly, the activation of the cerebellum was frequently reported for language- and emotion-related tasks (Stoodley and Schmahmann, 2009) and thus may represent a general increase of semantic and emotional processing of verbal stimuli with their increasing impact.

With regard to categorical comparisons of verbal and nonverbal stimuli, irrespective of the subsequent judgment, we could precisely replicate recent findings by Zaki et al. (2010) demonstrating domain-specific neural systems recruited when drawing inferences about emotional states of others based on either verbal or nonverbal social cues. A network related to mind state attribution including the dmPFC, the left PC/PCC and the bilateral temporal pole, as well as a left-lateralized network including inferior frontal, temporal and angular cortices associated with semantic processing (Price, 2000), were more strongly activated by verbal than by nonverbal stimuli. In contrast, nonverbal as compared to verbal stimuli more strongly engaged the right fronto-parietal cortex corresponding to the putative human mirror neuron system (Rizzolatti and Craighero, 2004), as well as the right posterior STS, the bilateral FFG and the bilateral middle temporal gyrus including the area V5/MT+ involved in face and movement perception (Kanwisher and Yovel, 2006; Pelphrey et al., 2005; Wilms et al., 2005). Thus, our data support the notion that both the mentalizing and the mirror neuron system are involved in the general processing of social information about others, but obviously with different priorities for different domains (Zaki et al., 2010).

Critically, Zaki et al. (2010) also showed that when drawing inferences based on conflicting pairs of verbal and nonverbal information, activity in the right frontoparietal cortex and pSTS correlated with the relative reliance on nonverbal cues, whereas the activity in the left angular gyrus and mPFC correlated with the relative reliance on verbal cues. These results, however, must not be regarded as inconsistent with the domain-specific parametric modulation findings reported here because the two studies explored two different types of cognitive processes, namely person evaluation as opposed to inferences about emotional states of others. Moreover, the correlation of the activity in the amygdala with nonverbal and in the PC/PCC with verbal stimuli reported here was based on the strength of impression resulting from differentially salient unimodally presented information and not on the relative reliance on cues presented in a multimodal fashion.

Noteworthy, the activity in the dmPFC was not modulated by the increasing intensity of judgments for any domain, but was categorically stronger for processing verbal as compared to nonverbal person information. Thus, this finding provides additional evidence for the proposal that the dmPFC is not essential for the evaluative component of impression formation (Schiller et al., 2009). Rather, the dmPFC appears to be related to the general inferential processing of social information. Within the verbal domain, this inferential processing seems to occur regardless of information's diagnostic value as long as the instruction to form an impression is explicitly given evoking the continuous need to monitor social meanings (Mitchell et al., 2006). Similarly, in situations that specifically require an identification of non-observable mental states such as assessing deceptive intentions (Grezes et al., 2004a), false beliefs (Grezes et al., 2004b), reasons for actions (Spunt et al., 2011), moment-to-moment emotional states (Zaki et al., 2009) or social relations (Iacoboni et al., 2004) the dmPFC has been recruited by nonverbal social cues as well. However, without such an explicit need for sophisticated inferential computation, non-verbal stimuli may convey observable and expressive cues therefore engaging the dmPFC to a lesser extent (Spunt et al., 2011; Zaki et al., 2010).

With respect to limitations of the study, it is important to note that both the source of information and the semantic content differed between the two domains: While nonverbal stimuli implied a "self-report" with the target person presenting herself actively by the display of communicative expression and gesture, verbal stimuli were reputation-based and referred to descriptions of social actions. This approach was chosen because of its ecological validity as in everyday life we are frequently confronted with reputation-based verbal information about other persons' actions and nonverbal cues that are directly observed. Furthermore, verbal self-reports could induce the impression of target's self-projection that could influence the creditability of the given information. Although it is not indisputable that the differential SoE-effects for the two domains of information were neither influenced by the source of information nor by the semantic content, the comparison of the SoE-effect between the two domains as such is still valid because the SoE was computed separately within each domain. Furthermore, the differential recruitment of distant brain regions for the two domains is consistent with previous research in the related field as described above. However, in future studies the source of social information should be taken into account, for example, by using statements about controversial topics instead of action descriptions as verbal stimuli. Such statements would indicate a self-report comparable to the nonverbal domain thereby avoiding problems with creditability. The difference between the semantic contents referring to actions or opinions on the one hand and to expressive nonverbal signals on the other is more difficult to overcome, as these differences are inextricably constitutive of the verbal and nonverbal domain.

Another limitation is given by the use of female virtual characters only. This procedure was chosen in order to constrain the experimental design to the focus on the SoE effect by disregarding possible effects of the gender of the target person. However, it seems unlikely that similar effects would not occur also for male targets, because exactly such evaluation-related effects, but without a strict differentiation of the information domain, have been demonstrated in a study by Schiller et al. (2009), which used male target persons only and a gender-mixed sample of participants.

Furthermore, we only report the peaks of activation of isolated neural regions that do not provide any insights into the underlying neural networks. Further neuroimaging research should focus on methods targeting functional and anatomical connectivity in order to enrich our understanding of the neural mechanisms also on a network level of description. These methods could for example help to identify possible influences of increased attention to more informative and diagnostic social information resulting in more extreme judgments, which are not directly evident from the reported SoE effects.

Conclusions

The present study provides evidence for neurofunctional dissociation between the processing of verbal and nonverbal social information during interpersonal impression formation. Our results show that behaviorally similar social cognitive operations were driven by distinct neural networks when taking into account the kind of available information. While the influence of verbal stimuli on interpersonal judgments appears to rely on the PC/PCC, previously associated with mental state inferences, nonverbal social information shapes

subsequent impression formation by the specific involvement of the amygdala, known to play a central role in automatic, affective processing. Instead of delineating these neurofunctional dissociations, however, in terms of independent dichotomies, it rather seems useful to characterize them as complementary parts of a complex interaction related to additional cognitive functions such as attention and memory. To explore these aspects further will be an important objective of future research. The question to what extent rapid, affective processes determine our social judgments and how this may relate to the presence of visual images has far reaching implications given the influence of impression formation on future expectations, decisions and behavior toward other persons. Due to the wide presence and increasing availability of visually transmitted information in today's media, this question is likely to take on even greater significance in the future.

Acknowledgments

References

Adolphs, R., Tranel, D., Damasio, A.R., 1998. The human amygdala in social judgment. Nature 393, 470–474.

Amaral, D.G., 2003. The amygdala, social behavior, and danger detection. Ann. N. Y. Acad. Sci. 1000, 337–347.

Amaral, D.G., Bauman, M.D., Schumann, C.M., 2003. The amygdala and autism: implications from non-human primate studies. Genes Brain Behav. 2, 295–302.

Ambady, N., Bernieri, F., Richeson, J., 2000. Towards a histology of social behavior: judgmental accuracy from thin slices of behavior. In: Zanna, M.P. (Ed.), Advances in Experimental Social Psychology, pp. 201–272.

Amodio, D.M., Frith, C.D., 2006. Meeting of minds: the medial frontal cortex and social cognition. Nat. Rev. Neurosci. 7, 268–277.

Anders, S., Eippert, F., Weiskopf, N., Veit, R., 2008. The human amygdala is sensitive to the valence of pictures and sounds irrespective of arousal: an fMRI study. Soc. Cogn. Affect. Neurosci. 3, 233–243.

Cunningham, W.A., Raye, C.L., Johnson, M.K., 2004. Implicit and explicit evaluation: FMRI correlates of valence, emotional intensity, and control in the processing of attitudes. J. Cogn. Neurosci. 16, 1717–1729.

Cunningham, W.A., Van Bavel, J.J., Johnsen, I.R., 2008. Affective flexibility: evaluative processing goals shape amygdala activity. Psychol. Sci. 19, 152–160.

Delgado, M.R., Frank, R.H., Phelps, E.A., 2005. Perceptions of moral character modulate the neural systems of reward during the trust game. Nat. Neurosci. 8, 1611–1618.

Engell, A.D., Haxby, J.V., Todorov, A., 2007. Implicit trustworthiness decisions: automatic coding of face properties in the human amygdala. J. Cogn. Neurosci. 19, 1508–1519.

Evans, J.S., 2008. Dual-processing accounts of reasoning, judgment, and social cognition. Annu. Rev. Psychol. 59, 255–278.

Freeman, J.B., Schiller, D., Rule, N.O., Ambady, N., 2010. The neural origins of superficial and individuated judgments about ingroup and outgroup members. Hum. Brain Mapp. 31, 150–159.

Gerber, A.J., Posner, J., Gorman, D., Colibazzi, T., Yu, S., Wang, Z., Kangarlu, A., Zhu, H., Russell, J., Peterson, B.S., 2008. An affective circumplex model of neural systems subserving valence, arousal, and cognitive overlay during the appraisal of emotional faces. Neuropsychologia 46, 2129–2139.

Grezes, J., Frith, C., Passingham, R.E., 2004a. Brain mechanisms for inferring deceit in the actions of others. J. Neurosci. 24, 5500–5505.

Grezes, J., Frith, C.D., Passingham, R.E., 2004b. Inferring false beliefs from the actions of oneself and others: an fMRI study. Neuroimage 21, 744–750.

Hariri, A.R., Tessitore, A., Mattay, V.S., Fera, F., Weinberger, D.R., 2002. The amygdala response to emotional stimuli: a comparison of faces and scenes. Neuroimage 17, 317–323.

Harris, L.T., Todorov, A., Fiske, S.T., 2005. Attributions on the brain: neuro-imaging dispositional inferences, beyond theory of mind. Neuroimage 28, 763–769.

Iacoboni, M., Lieberman, M.D., Knowlton, B.J., Molnar-Szakacs, I., Moritz, M., Throop, C.J., Fiske, A.P., 2004. Watching social interactions produces dorsomedial prefrontal and medial parietal BOLD fMRI signal increases compared to a resting baseline. Neuroimage 21, 1167–1173.

Kanwisher, N., Yovel, G., 2006. The fusiform face area: a cortical region specialized for the perception of faces. Philos. Trans. R. Soc. Lond. B Biol. Sci. 361, 2109–2128.

Kastner, S., Ungerleider, L.G., 2000. Mechanisms of visual attention in the human cortex. Annu. Rev. Neurosci. 23, 315–341.

Kraemer, N.C., 2008. Nonverbal communication. In: Blascovich, J.J., Hartel, C.R. (Eds.), Human Behavior in Military Contexts. National Academic Press, Washington, pp. 150–188.

Kuzmanovic, B., Schilbach, L., Lehnhardt, F.-G., Bente, G., Vogeley, K., 2011. A matter of words: impact of verbal and nonverbal information on impression formation in high-functioning autism. Res. Autism Spectr. Disord. 5, 604–613.

Lambert, S., Sampaio, E., Scheiber, C., Mauss, Y., 2002. Neural substrates of animal mental imagery: calcarine sulcus and dorsal pathway involvement—an fMRI study. Brain Res. 924, 176–183.

Lieberman, M.D., 2010. Social cognitive neuroscience. In: Fiske, S.T., Gilbert, D.T., Lindzey, G. (Eds.), Handbook of Social Psychology. McGraw Hill, New York, pp. 143–193.

Lieberman, M.D., Gaunt, R., Gilbert, D.T., Trope, Y., 2002. Reflection and reflexion: a social cognitive neuroscience approach to attributional inference. Adv. Exp. Soc. Psychol. 34, 199–249.

Lieberman, M.D., Hariri, A., Jarcho, J.M., Eisenberger, N.I., Bookheimer, S.Y., 2005. An fMRI investigation of race-related amygdala activity in African-American and Caucasian-American individuals. Nat. Neurosci. 8, 720–722.

Maddock, R.J., 1999. The retrosplenial cortex and emotion: new insights from functional neuroimaging of the human brain. Trends Neurosci. 22, 310–316.

Maddock, R.J., Garrett, A.S., Buonocore, M.H., 2003. Posterior cingulate cortex activation by emotional words: fMRI evidence from a valence decision task. Hum. Brain Mapp. 18, 30–41.

Mitchell, J.P., Heatherton, T.F., Macrae, C.N., 2002. Distinct neural systems subserve person and object knowledge. Proc. Natl. Acad. Sci. U. S. A. 99, 15238–15243.

Mitchell, J.P., Neil Macrae, C., Banaji, M.R., 2005. Forming impressions of people versus inanimate objects: social-cognitive processing in the medial prefrontal cortex. Neuroimage 26, 251–257.

Mitchell, J.P., Cloutier, J., Banaji, M.R., Macrae, C.N., 2006. Medial prefrontal dissociations during processing of trait diagnostic and nondiagnostic person information. Soc. Cogn. Affect. Neurosci. 1, 49–55.

Ochsner, K.N., Bunge, S.A., Gross, J.J., Gabrieli, J.D., 2002. Rethinking feelings: an FMRI study of the cognitive regulation of emotion. J. Cogn. Neurosci. 14, 1215–1229.

Ochsner, K.N., Ray, R.D., Cooper, J.C., Robertson, E.R., Chopra, S., Gabrieli, J.D., Gross, J.J., 2004. For better or for worse: neural systems supporting the cognitive down- and up-regulation of negative emotion. Neuroimage 23, 483–499.

Ochsner, K.N., Beer, J.S., Robertson, E.R., Cooper, J.C., Gabrieli, J.D., Kihsltrom, J.F., D'Esposito, M., 2005. The neural correlates of direct and reflected self-knowledge. Neuroimage 28, 797–814.

Pelphrey, K.A., Morris, J.P., Michelich, C.R., Allison, T., McCarthy, G., 2005. Functional anatomy of biological motion perception in posterior temporal cortex: an FMRI study of eye, mouth and hand movements. Cereb. Cortex 15, 1866–1876.

Phan, K.L., Wager, T., Taylor, S.F., Liberzon, I., 2002. Functional neuroanatomy of emotion: a meta-analysis of emotion activation studies in PET and fMRI. Neuroimage 16, 331–348.

Phelps, E.A., LeDoux, J.E., 2005. Contributions of the amygdala to emotion processing: from animal models to human behavior. Neuron 48, 175–187.

Phelps, E.A., O'Connor, K.J., Cunningham, W.A., Funayama, E.S., Gatenby, J.C., Gore, J.C., Banaji, M.R., 2000. Performance on indirect measures of race evaluation predicts amygdala activation. J. Cogn. Neurosci. 12, 729–738.

Posner, J., Russell, J.A., Gerber, A., Gorman, D., Colibazzi, T., Yu, S., Wang, Z., Kangarlu, A., Zhu, H., Peterson, B.S., 2009. The neurophysiological bases of emotion: an fMRI study of the affective circumplex using emotion-denoting words. Hum. Brain Mapp. 30, 883–895.

Price, C.J., 2000. The anatomy of language: contributions from functional neuroimaging. J. Anat. 197 (Pt. 3), 335–359.

Rizzolatti, G., Craighero, L., 2004. The mirror-neuron system. Annu. Rev. Neurosci. 27, 169–192.

Said, C.P., Baron, S.G., Todorov, A., 2009. Nonlinear amygdala response to face trustworthiness: contributions of high and low spatial frequency information. J. Cogn. Neurosci. 21, 519–528.

Sander, K., Scheich, H., 2001. Auditory perception of laughing and crying activates human amygdala regardless of attentional state. Brain Res. Cogn. Brain Res. 12, 181–198.

Sander, D., Grafman, J., Zalla, T., 2003. The human amygdala: an evolved system for relevance detection. Rev. Neurosci. 14, 303–316.

Schiller, D., Freeman, J.B., Mitchell, J.P., Uleman, J.S., Phelps, E.A., 2009. A neural mechanism of first impressions. Nat. Neurosci. 12, 508–514.

Schulman, G.L., Fiez, J.A., Corbetta, M., Buckner, R.L., Miezin, F.M., Raichle, M.E., Petersen, S.E., 1997. Common blood flow changes across visual tasks: II. Decreases in cerebral cortex. J. Cogn. Neurosci. 9, 648–663.

Serences, J.T., 2004. A comparison of methods for characterizing the event-related BOLD timeseries in rapid fMRI. Neuroimage 21, 1690–1700.

Sergerie, K., Chochol, C., Armony, J.L., 2008. The role of the amygdala in emotional processing: a quantitative meta-analysis of functional neuroimaging studies. Neurosci. Biobehav. Rev. 32, 811–830.

Spunt, R.P., Satpute, A.B., Lieberman, M.D., 2011. Identifying the what, why, and how of an observed action: an fMRI study of mentalizing and mechanizing during action observation. J. Cogn. Neurosci. 23, 63–74.

Stoodley, C.J., Schmahmann, J.D., 2009. Functional topography in the human cerebellum: a meta-analysis of neuroimaging studies. Neuroimage 44, 489–501.

Sugiura, M., Gotoh, R., Okada, K., Yamaguchi, K., Itoh, M., Fukuda, H., Kawashima, R., 2004. Target dependency of brain mechanism involved in dispositional inference: a PET study. Neuroimage 21, 1377–1386.

Todorov, A., 2008. Evaluating faces on trustworthiness: an extension of systems for recognition of emotions signaling approach/avoidance behaviors. Ann. N. Y. Acad. Sci. 1124, 208–224.

Todorov, A., Engell, A.D., 2008. The role of the amygdala in implicit evaluation of emotionally neutral faces. Soc. Cogn. Affect. Neurosci. 3, 303–312.

Todorov, A., Baron, S.G., Oosterhof, N.N., 2008. Evaluating face trustworthiness: a model based approach. Soc. Cogn. Affect. Neurosci. 3, 119–127.

Uleman, J.S., Adil Saribay, S., Gonzalez, C.M., 2008. Spontaneous inferences, implicit impressions, and implicit theories. Annu. Rev. Psychol. 59, 329–360.

Vuilleumier, P., Pourtois, G., 2007. Distributed and interactive brain mechanisms during emotion face perception: evidence from functional neuroimaging. Neuropsychologia 45, 174–194.

Watzlawick, P., Bavelas, J.H., Jackson, D.D., 1967. Pragmatics of Human Communication: a Study of Interactional Patterns, Pathologies, and Paradoxes. Norton, New York.

Wilms, M., Eickhoff, S.B., Specht, K., Amunts, K., Shah, N.J., Malikovic, A., Fink, G.R., 2005. Human V5/MT+: comparison of functional and cytoarchitectonic data. Anat. Embryol. (Berl.) 210, 485–495.

Winston, J.S., Strange, B.A., O'Doherty, J., Dolan, R.J., 2002. Automatic and intentional brain responses during evaluation of trustworthiness of faces. Nat. Neurosci. 5, 277–283.

Zaki, J., Weber, J., Bolger, N., Ochsner, K., 2009. The neural bases of empathic accuracy. Proc. Natl. Acad. Sci. U. S. A. 106, 11382–11387.

Zaki, J., Hennigan, K., Weber, J., Ochsner, K.N., 2010. Social cognitive conflict resolution: contributions of domain-general and domain-specific neural systems. J. Neurosci. 30, 8481–8488.

Zald, D.H., 2003. The human amygdala and the emotional evaluation of sensory stimuli. Brain Res. Brain Res. Rev. 41, 88–123.

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.