The Neural Networks of Subjectively Evaluated Emotional Conflicts

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Abstract: Previous work on the neural underpinnings of emotional conflict processing has largely focused on designs that instruct participants to ignore a distracter which conflicts with a target. In contrast, this study investigated the noninstructed experience and evaluation of an emotional conflict, where positive or negative cues can be subjectively prioritized. To this end, healthy participants freely watched short film scenes that evoked emotional conflicts while their BOLD responses were measured. Participants' individual ratings of conflict and valence perception during the film scenes were collected immediately afterwards, and the individual ratings were regressed against the BOLD data. Our analyses revealed that (a) amygdala and medial prefrontal cortex were significantly involved in prioritizing positive or negative cues, but not in subjective evaluations of conflict per se, and (b) superior temporal sulcus (STS) and inferior parietal lobule (IPL), which have been implicated in social cognition and emotion control, were involved in both prioritizing positive or negative cues and subjectively evaluating conflict, and may thus constitute "hubs" or "switches" in emotional conflict processing. Psychophysiological interaction (PPI) analyses further revealed stronger functional connectivity between IPL and ventral prefrontal—medial parietal areas in prioritizing negative cues, and stronger connectivity between STS and dorsal-rostral prefrontal—medial parietal areas in prioritizing positive cues. In sum, our results suggest that IPL and STS are important in the subjective evaluation of complex conflicts and influence valence prioritization via prefrontal and parietal control centers. *Hum Brain Mapp 37:2234–2246, 2016.* © **2016 Wiley Periodicals, Inc.**

Additional Supporting Information may be found in the online version of this article.

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INTRODUCTION

Everyday human life contains a wealth of complex, multimodal socio-emotional cues that we need to make meaning of in order to function. One particular challenge is processing conflicting or contradictory cues of divergent implicit valence. For instance, a person may portray a positive emotion via their facial expression, but verbally supply negative content alongside it. We perceive both the positive and the negative cue at the same time, and quickly need to figure out which one should be prioritized. Failure to adequately process such conflicting cues can fundamentally impair individual well-being and mental health [Campos et al., 2011]. Individuals suffering from depression and anxiety, for instance, display strong tendencies to interpret ambiguous cues negatively, causing them unnecessary worry and distress [Dearing and Gotlib, 2009; Enkel et al., 2010; Lawson et al., 2002]. In recent years, research on emotional conflict has been accumulating [Egner et al., 2008; Etkin et al., 2006, 2010; Hoyer et al., 2013; Jarcho et al., 2013; Rey et al., 2014; Waring et al., 2014].[1] To date, the neural networks of how to ignore a predefined distracting stimulus that conflicts with the target stimulus are thought to revolve around the amygdala, anterior cingulate (ACC) and medial prefrontal cortex (mPFC) [Egner et al., 2008; Etkin et al., 2006, 2010; Kanske and Kotz, 2011; Waring et al., 2014]. However, there is currently little evidence on the neural mechanisms underlying subjective, individual evaluation of a conflict that occurs in the absence of an a priori defined target stimulus. This question is particularly relevant if we consider the example above: it is not always obvious in everyday life which of the conflicting cues is the distracter and which is the target. We first need to figure out which of the cues to deem "relevant" and which "irrelevant" before we can proceed to ignore the task-irrelevant information. Such subjective evaluations do not necessarily require volitional control in real life, whereas volitional control is an essential component in task-based paradigms. This is readily apparent in recent studies [Seehausen et al., 2014; Watanabe et al., 2014; Zaki et al., 2010], which have let participants subjectively evaluate conflicts, but have instructed them to do so in a certain manner. These studies implicate superior temporal sulcus (STS), fusiform gyrus (FuG), posterior cingulate (PCC) and inferior parietal lobule (IPL) in socio-emotional conflict processing—regions which have also been implicated in the cognitive control of emotion [Ochsner et al., 2012].[2] Moreover, unlike in the case of ignoring a predefined distracter, subjectively evaluating conflicting cues can lead to individually different interpretations. There have also been efforts to parse out the neural mechanisms underlying the individual prioritization of some conflicting cues over others: Zaki et al. [2010] have investigated the prioritization of either a facial expression or its accompanying verbal description; Wittfoth et al. [2010] have investigated the prioritization of either positive or negative intonations that are accompanied by incongruent semantic content. However, it is not yet clear how neural underpinnings differ when positive or negative cues are prioritized regardless of the modality in which they are presented. In addition, accumulating evidence suggests that emotion and executive functions are inherently linked [Ochsner et al., 2012; Okon-Singer et al., 2013, 2014, 2015; Rohr et al., 2015], highlighting the possibility that conflict evaluation, an executive process, and valence prioritization, an emotion process, may rely on shared neural processes.

The current work is therefore designed to assess the neural mechanisms underlying prioritization of positive over negative cues and vice versa, in the course of subjective, individual evaluations of conflict within a naturalistic paradigm. Healthy participants freely watched short film scenes that evoked emotional conflicts in a functional magnetic resonance imaging (fMRI) experiment. These previously validated scenes were taken from Hollywood movies such as "Reservoir Dogs" [1992] and presented positive and negative affective inputs simultaneously, thus sharing main characteristics with other conflict elicitors such as Stroop tasks. In contrast to previous studies, participants were allowed to freely attend to whichever aspect of the presented films they wanted, and no task instruction, which could interfere with natural processing mechanisms by itself, was given. To assess arousal and ensure immersion in the film scenes, heart rate and skin conductance were simultaneously recorded. Based on a pilot study (see Supporting Information), participants rated their

[1]Also see Algom et al., 2004 on why emotional conflict tasks do not always measure conflict—for instance because stimuli in the paradigm do not actually conflict with each other.

[2]Although differentiations between the "terms emotion control," "cognitive control of emotion" and "emotion regulation" are sometimes made [see e.g. Grandey et al., 2005], they are commonly used interchangeably [see e.g. Ochsner and Gross, 2005 or Ochsner et al., 2012] as "control" can refer to both volitional or spontaneous regulation of one's own behavior, as well as to external demands that guide or require regulation of behavior. The regulation of emotional conflict when completing a Stroop task would be an example of the latter [see e.g. Etkin et al., 2010].

experience during the scenes post-hoc for valence and conflict. We expected that (a) the subjectively evaluated emotional conflict would engage a network of regions previously implicated in socio-emotional conflict processing, such as amygdala, ACC, PFC, STS and IPL and (b) prioritization of positive or negative cues would be reflected in differential activity and connectivity within this network.

MATERIALS AND METHODS

Participants

Twenty-seven healthy volunteers without any history of neurological, psychiatric or cardiovascular illnesses volunteered to participate in the study in return for payment. The study was approved by the local ethics board of the University of Leipzig and all participants provided written informed consent. All participants were right-handed, had normal or corrected-to-normal vision and had never received any formal film training or worked in the film industry. Participants were characterized with regard to familiarity with the scenes (3.76 ± 1.98; out of a maximum of 10 scenes), affinity for films (7.23 ± 1.27; maximum affinity = 10) and educational status (14.71 ± 1.49 years). They were further screened with the Positive And Negative Affect Schedule (PANAS) [Watson et al., 1988; German version: Krohne et al., 1996], the Emotion Regulation Questionnaire (ERQ) [Gross and John, 2003; German version: Abler and Kessler, 2009], the Interpersonal Reactivity Index (IRI) [Davis, 1980; German version: Paulus, 2009] and the Sensation Seeking Scale V (SSS-V) [Zuckerman, 1994; German version: Beauducel et al., 2003]; no outliers were detected. Two fMRI scans were excluded due to excessive head motion (>1.5 mm); one of the participants in addition showed nonresponsiveness in skin conductance (lack of identified changes >0.02 μS). Further, three heart rate recordings were excluded due to a combination of poor data quality and insufficient correction of the artifact induced by the MR. 25 skin conductance and 22 heart rate recordings, as well as 25 fMRI data sets (12 female, 13 male, age = 26.29 ± 3.23 years) were analyzed.

Stimuli

Ten previously validated film scenes between 1.5 and 3 min long were used as stimuli (see Supporting Information). As virtually all fiction stories start by setting up a conflict within or between characters and end when the conflict is resolved [Field, 1989; Seger, 1992], fiction films are good stimuli to induce an emotional conflict. All scenes presented positive and negative affective inputs simultaneously, either through only the visual or both the visual and the auditory domain, and could thus be expected to elicit an emotional conflict within the viewer. For example, one scene—taken from the film "Reservoir Dogs" (see complete list below)—features a man being tortured by another man who is speaking to him in a rather friendly fashion. Importantly, we chose scenes that present incongruent affective inputs simultaneously, as these share main characteristics with other conflict elicitors, such as Stroop tasks. The conflict presented in the scenes was not based on different emotions conveyed via different sensory modalities (e.g., auditory and visual), but inherent in the content (e.g., depictions of a situation which is negative for one person and positive for another, or a person's behavior that is incongruent with their facial expressions or gestures). In order to ensure maximum ecological validity and facilitate immersion, the selected films' fictional worlds were evaluated according to the typology of accessibility relations developed by Marie-Laure Ryan [Ryan, 1991]. In fiction theory, accessibility relations establish the extent to which fictional worlds are similar or different to the actual world we live in. The fictional world that most resembles the actual world is based on the "principle of minimal departure" [Dolezel, 1998]. All chosen films resembled the actual world by >90%. Further, as critical and commercial success is indicative of a universal, emotionally engaging experience, all films were critically acclaimed box-office successes: Black Swan (Director: Darren Aronofsky; Release: 2010), A Clockwork Orange (D: Stanley Kubrick; R: 1971/1987), Four Rooms (D: Allison Anders, Alexandre Rockwell, Robert Rodriguez, Quentin Tarantino; R: 1996), Funny Games (D: Michael Haneke, R: 1997), Funny Games U.S. (D: Michael Haneke, R: 2008), Inglourious Basterds (D: Quentin Tarantino; R: 2009), The Piano (D: Jane Campion, R: 1993), Pulp Fiction (D: Quentin Tarantino; R: 1994), Reservoir Dogs (D: Quentin Tarantino; R: 1992), True Romance (D: Tony Scott, R: 1994). Scenes from Hollywood films have previously successfully been used as fMRI stimuli [Eryilmaz et al., 2011; Hasson et al., 2004; Nummenmaa et al., 2012; Pehrs et al., 2014, 2015; Quirin et al., 2013; Raz et al., 2012, 2014; Straube et al., 2010].

Heart Rate and Skin Conductance

Heart rate and skin conductance were continuously recorded at a sampling rate of 5,000 Hz using a bipolar signal amplifier (Brain Products, Munich, Germany) in order to assess autonomic arousal as an objective measure of emotional arousal [Codispoti et al., 2008; Cuthbert et al., 2000; Lane et al., 2009; Mauss and Robinson, 2009; Santarcangelo et al., 2012]. Skin conductance was recorded at the volar surface of the proximal phalanges of index and middle finger of the left hand [Santarcangelo et al., 2012], while heart rate was recorded in a modified Lead II configuration in the behavioral experiment [Codispoti et al., 2008] and on the participant's back in the MR to avoid breathing artifacts. Before placement, participants were instructed to clean the electrode sites to remove excess oils, and, when necessary, were given a shaver to remove any excess chest hair. Recordings then started after optimal adjustment when the signal appeared clean upon visual inspection. Heart rate and skin conductance recordings were connected to the Presentation software that played the film scenes, and triggers were used to indicate start and end of the scenes. Baseline was set as the 10 s prior to each viewing.

fMRI Experiment

FMRI data were collected on a 3T Siemens Magnetom Tim Trio (Siemens, Erlangen, Germany) scanner using a standard echo-planar imaging protocol (885 volumes, TR = 2,000 ms, TE = 25 ms, flip angle = 90°, 64 × 64 matrix, voxel dimensions 3 × 3 × 4 mm^3). Film scenes were presented in six pseudo-randomized orders via a mirror using Presentation 14.9 (Neurobehavioral Systems, San Francisco, CA, USA), a projector and MR-compatible headphones. Participants were familiarized with the kind of material they would see using a test scene (Death Proof; D: Q. Tarantino; R: 2007) presented in the scanner, during which volume was adjusted. Scenes were separated by 45 s breaks, during which the screen remained dark. To exclude the possibility that the process of rating influences the experience of emotion [Lieberman et al., 2007], as well as neural patterns (such as increasing activity in motor cortex, anterior cingulate and insula) [see e.g., Hutcherson et al., 2005], participants were asked to watch the film scenes as they normally would. Immediately after the fMRI scanning, participants were shown the scenes again in the same order, in a separate testing room away from the scanner. This time they were asked to rate their experience using the scroll-wheel of a computer mouse (Fig. 1). This rating procedure was validated in a behavioral pilot study (see Supporting Information). The instructions [see Nummenmaa et al., 2012 for comparison] were "watch the film scenes again and continuously rate how positive or negative you just felt when you watched the scenes in the scanner." Each scene thus received continuous ratings along a red-and-blue colored positive-negative spectrum by which the participant was able to indicate at any given time point within the scene whether he or she was having a more positive or more negative experience during the scene, and how positive or how negative it was (open range, +29 to −29 visible on screen next to the film scenes; no number display). These ratings were recorded at a sampling rate of 35 Hz. Further, at the end of each scene, it was given a subjective conflict rating by the participant (open range, 0–58 visible on screen; no number display). The instruction was "please rate how emotionally conflicting the scenes were for you when you watched them in the scanner," and emotional conflict was defined as the presence of ambiguous or contradictory emotions related to the story in the movie. For both the instructions of the conflict and valence ratings, we asked participants to repeat back to us in their own words what they were supposed to do in order to make sure that they had understood correctly. Participants then tested practicability of the rating procedure using the test scene (the excerpt from

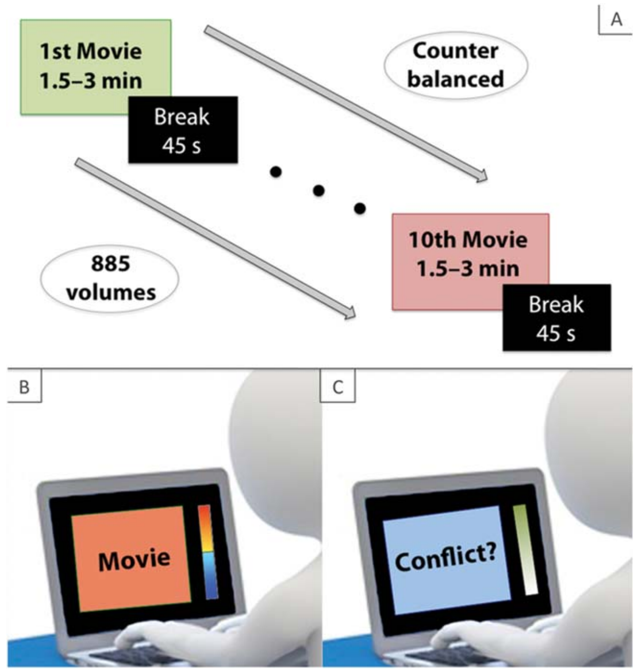

Figure 1.
Paradigm and rating procedure. (**A**) Ten film scenes were presented in six pseudo-randomized orders, separated by 45 s breaks, during which the screen remained dark. Heart rate, skin conductance and BOLD signal were continuously recorded. (**B**) Each scene received continuous ratings along a red-and-blue colored positive-negative spectrum by which the participant was able to indicate at any given time point within the scene whether he or she was having a more positive or more negative experience during the scene (open range, +29 to −29 visible on screen next to the film scenes; no number display). (**C**) Each scene was given a subjective conflict rating by the participant (open range, 0–58 visible on screen; no number display). [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

Death Proof) during which they were monitored by the experimenter and had the chance to ask further questions. Anatomical scans were acquired in a separate session using a T1-weighted 3D MP-RAGE sequence (FOV = 256 × 240 mm^2, voxel dimensions 1 × 1 × 1.5 mm^3).

Data Analysis

Continuous ratings were analyzed in SPSS 20 (IBM Corp., Armonk, NY, USA) with an original sampling rate of 35 Hz and downsampled to 2 s for fMRI using MATLAB R2009b (Mathworks, Natick, MA, USA). Skin conductance and heart rate were extracted using Brain Vision Analyzer 2 (Brain Products, Munich, Germany). MR-artifact correction and further analysis to determine average skin conductance level per scene (vs. baseline), and average heart rate per scene (vs. baseline) were done using in-house MATLAB scripts. fMRI data were preprocessed and analyzed using FSL 4.1.5 [Jenkinson et al., 2012; Smith et al., 2004]. Preprocessing included slice-timing correction, motion correction, spatial smoothing (5 mm Gaussian kernel), a highpass filter of 180 s, and linear registration to the participant's anatomical scan and 2 mm isotropic MNI152 standard space. A first analysis was conducted to explore which brain regions reflected the participants' subjective conflict evaluation during the scenes. For this analysis, we used the demeaned conflict score that each of the ten scenes had received as predictors in the individual-level analysis. We then employed a mixed-effects group-level regression, which included demeaned gender and familiarity with the scenes as covariates of no interest, and thresholded results at voxelwise z score >2.3 and $P < 0.05$ clusterwise correction using Gaussian random field (GRF) theory. A second analysis was conducted to explore which brain regions were significantly more involved in prioritizing negative over positive cues during the scenes and vice versa. For this analysis, we used the demeaned continuous valence ratings for each scene as predictors in the individual-level analysis for individual main effects of prioritizing positive versus negative cues. We then employed another mixed-effects group-level regression ($P < 0.05$). To examine activity related to both conflict and valence, and to probe the postulated inherent link between underlying emotion and executive processes, we further carried out a conjunction analysis that mapped the overlap between the first two analyses at their respective thresholds. Results of this analysis subsequently served as seed regions in a psychophysiological interaction (PPI) analysis [Friston et al., 1997; O'Reilly et al., 2012] in order to explore the functional networks underlying differences between the prioritization of positive and negative cues further. PPI analysis identifies activity in brain regions that is explained by the influence of the interaction between activity in another brain region (the physiological parameter) and the experiment (the psychological parameter). Results from this analysis indicate that connectivity between a seed region and the identified region changes significantly as a function of task condition or state, i.e. prioritizing positive or negative cues. We set up the PPI analysis matrix according to McLaren et al. [2012] using four explanatory variables in the individual-level: (1) the psychological parameter: individual continuous ratings along the positive-negative spectrum for a main effect of prioritizing positive vs. negative cues, with every positive rating falling into the "positive prioritization" condition and every negative rating falling into the "negative prioritization" condition; (2) the physiological parameter: individual time course of each seed; (3) the interaction between the psychological parameter and the physiological parameter; and (4) individual continuous absolute ratings for a main effect of cue prioritization, regardless of valence, in order to pick up variance shared by prioritization of positive and negative cues. The interaction term yields connectivity between the seed region and regions that is significantly different between prioritizing positive and negative cues. Again we employed a mixed-effects group-level regression ($P < 0.05$, corrected for two comparisons: $P < 0.025$).

RESULTS

Ratings and Autonomic Measures

All film scenes received a high conflict score (mean $= 37.21 \pm 8.04$). Further, every scene received both positive and negative ratings from the participants within its time course, and every participant had rated both positively and negatively in their continuous ratings. Average conflict evaluation and average valence prioritization were not correlated across subjects ($r^2 = 0.018$ $P > 0.45$ n.s.), suggesting that conflict evaluation was not predicted by dominance in the prioritization of either valence.[3] Skin conductance and heart rate both markedly increased from baseline, indicating high autonomic arousal across participants (average baseline skin conductance: 20.83 μS, average increase 3.04; average baseline heart rate: 75.3 bpm, average increase 3.88). No significant differences in skin conductance and heart rate were observed with regard to prioritization of either positive or negative cues, meaning valence prioritization was not confounded by differences in arousal. These data replicated results from the pilot study (see Supporting Information).

Differential Brain Activity for Prioritization of Positive versus Negative Cues

Several brain regions were differentially active when positive cues were prioritized over negative cues, and vice versa (Table I and Fig. 2). STS, temporal pole (TP), posterior amygdala and anterior hippocampus, occipital pole (OP), and dorsomedial PFC (dmPFC) showed enhanced activity during prioritization of positive as compared to negative cues within the emotionally conflicting scenes. In contrast, IPL and insula were significantly more active during prioritization of negative as compared to positive cues within the emotionally conflicting scenes.

Subjective Conflict Evaluation and Brain Activity

Neural activity correlated with the subjective conflict evaluation per scene in the following regions: FuG, IPL, inferior lateral occipital complex (LOC), precuneus, OP and cerebellar VIII all increased in activity as subjective

[3]Recent theories postulate that dealing with conflicting information may be a predominantly negative experience in itself [Dreisbach and Fischer, 2012 or Fritz and Dreisbach, 2013; but also see Fritz and Dreisbach, 2015].

TABLE I. Increases in functional activity during prioritization of positive over negative and negative over positive cues

	Lat	Area	BA	Voxels	*P*-Value	Z-Max	*x*	*y*	*z*
pos > neg	L	STS	22	4,503	<0.000001	4.9	−46	−34	−2
	L	Temporal Pole	38			4.52	−52	8	−26
	L	Amygdala/Hippocampus	-, 35			3.25	−28	0	−28
pos > neg	R	STS	22	2,257	<0.000001	4.19	46	−22	−4
	R	Temporal Pole	38			4.05	56	10	−22
pos > neg	L	Occipital Pole	17, 18	1,264	<0.000001	4.6	−22	−102	−10
pos > neg	R	Occipital Pole	17, 18	1,048	<0.000001	5.07	30	−98	−6
pos > neg	L	dmPFC	8	461	0.0104	3.82	−12	52	28
neg > pos	R	IPL	39, 40	1,729	<0.000001	4.19	60	−22	36
neg > pos	L	IPL	39, 40	1,028	0.0000013	3.87	−58	−38	34
neg > pos	R	Insula	16	473	0.0088	3.83	50	14	0

BA = Brodmann Area; dmPFC = dorsomedial Prefrontal Cortex; IPL = Inferior Parietal Lobule; STS = Superior Temporal Sulcus.

conflict increased, while activity in the STS, superior LOC and superior frontal sulcus (SFS) decreased in activity as subjective conflict increased (Table II and Fig. 3).

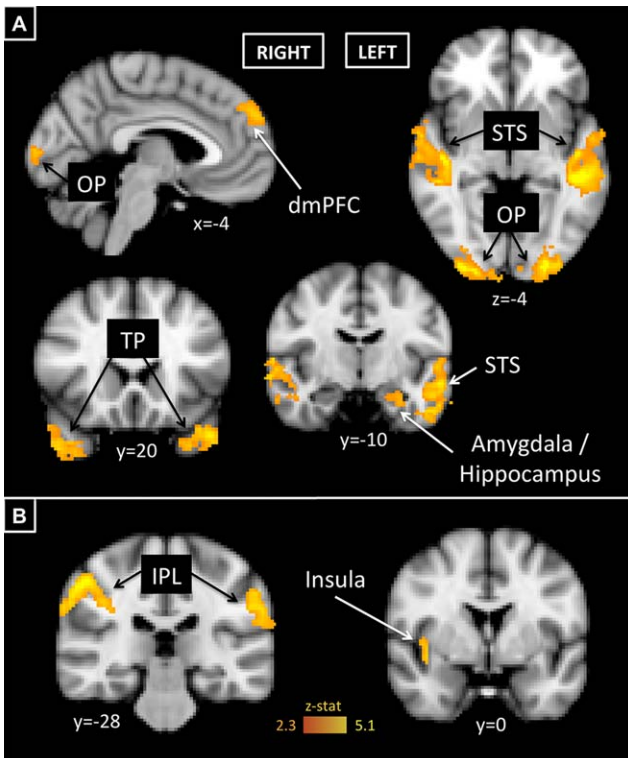

Figure 2.
Increases in functional activity during prioritization of (A) positive over negative cues and (B) negative over positive cues. dmPFC = dorsomedial prefrontal cortex; IPL = supramarginal gyrus/inferior parietal lobule; OP = occipital pole; STS = superior temporal sulcus; TP = temporal pole. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

Brain Regions Common to Conflict Evaluation and Valence Prioritization

A conjunction analysis across all significant results from both the first analysis on valence and the second analysis on conflict revealed two regions that were significantly related to both conflict and valence (Fig. 4). These were left STS, which was associated with both greater activity during prioritization of positive cues, as well as a decrease in activity as conflict increased; and right IPL, which was associated with both greater activity during prioritization of negative cues, as well as an increase in activity as conflict increased.

Differential Connectivity for Prioritization of Positive versus Negative Cues

The PPI analysis, which used the two regions common to conflict evaluation and valence prioritization as seeds, yielded differential connectivity results for prioritization of positive or negative cues within the conflicting scenes (Tables III and IV, Fig. 5). During prioritization of positive cues, left STS was significantly connected to a medial prefrontal-parietal cluster spanning dorsal-rostral PFC and dorsal-rostral ACC, PCC and precuneus. It was further connected to the right IPL and subcortically to bilateral thalamus and caudate. During prioritization of negative cues, right IPL was significantly connected to an occipital-parietal cluster spanning bilateral FuG, lingual gyrus (LG) and OP, as well as cuneus and precuneus. In addition, it was connected to a prefrontal cluster of ventral mPFC and ventral ACC bilaterally.

DISCUSSION

The present study aimed to elucidate the neural networks underlying subjective, individual evaluation of socio-emotional conflict processing, in the absence of an a priori defined target stimulus and irrelevant distracters. Moreover, while neural underpinnings have been shown to be differential depending on the prioritized input

TABLE II. Correlation between functional activity and the subjective conflict evaluation scores

	Lat	Area	BA	Voxels	*P*-Value	Z-Max	*x*	*y*	*z*
positive	L	Inferior LOC	19	2,926	<0.000001	4.07	−36	−74	2
positive	L	Fusiform Gyrus	37			4.06	−32	−82	−20
positive	L	Occipital Pole	17, 18			3.73	−12	−92	−14
positive	L	Cerebellar VIII	-	1,518	<0.000001	4.41	−26	−44	−50
positive	R	Inferior LOC	19	1,263	<0.000001	4.65	50	−72	−8
positive	R	IPL	39, 40	1,202	<0.000001	4	64	−20	34
positive	R	Precuneus	7	487	0.00537	3.8	−6	−58	68
positive	R	Cerebellar VIII	-	413	0.0154	3.81	12	−72	−46
negative	L	STS	22	985	0.0000012	3.96	−50	−20	−6
negative	L	Superior LOC	19	783	0.000122	4.09	−54	−68	26
negative	L	SFS	10	574	0.00166	4.16	−8	32	60

BA = Brodmann Area; LOC = Lateral Occiptal Complex; IPL = Inferior Parietal Lobule; STS = Superior Frontal Sulcus; STS = Superior Temporal Sulcus.

modality, and also on valence within a prioritized input modality, it is not yet clear how neural underpinnings differ when positive or negative cues are prioritized regardless of the modality in which they are presented. We addressed these questions by measuring healthy participants' BOLD responses and individual ratings of conflict-eliciting film scenes, which depicted socio-emotional cues. Regression analysis using participants' ratings revealed that prioritizing either positive or negative cues was associated with activity in regions previously implicated in social and/or emotional conflict processing, including the amygdala, dmPFC and insula. A separate analysis using

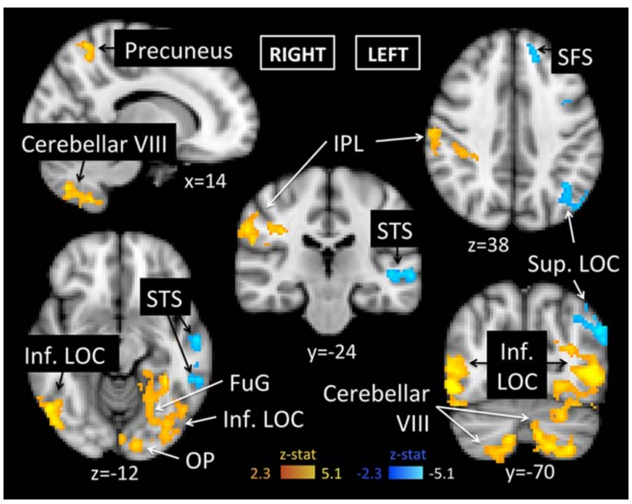

Figure 3.

Correlation between subjective conflict evaluation scores and functional activity. FuG = fusiform gyrus; Inf. LOC = inferior lateral occiptal complex; OP = occipital pole; IPL = supramarginal gyrus/inferior parietal lobule; SFS = superior frontal sulcus; STS = superior temporal sulcus; Sup. LOC = superior lateral occipital complex. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

participants' ratings of subjective conflict evaluation correlated with activity in regions linked to social cognition within conflict processing, such as STS, IPL and FuG. It is noteworthy that STS and IPL were involved in both valence prioritization and conflict evaluation, indicating that these regions may constitute high-degree nodes in socio-emotional conflict processing [see Sporns et al., 2007; van den Heuvel and Sporns, 2013, for comprehensive review and elaboration on neural networks]. These regions may integrate input coming from diverse neural regions, including sensory information from various sensorimotor regions, emotional information from limbic regions, and cognitive information related to executive inhibition from frontal regions. As a result, STS and IPL may act as central connecting hubs that influence the activation of networks related to positive-rewarding or negative-unpleasant feelings. In line with this idea, PPI analyses further revealed stronger functional connectivity between IPL and ventral prefrontal—medial parietal areas in prioritizing negative cues, and stronger functional connectivity between STS and dorsal-rostral prefrontal—medial parietal areas in prioritizing positive cues, suggesting that IPL and STS may in part influence valence prioritization via frontoparietal control centers.

A common "Conflict Network": Brain Regions Involved in Prioritization of Positive or Negative Cues and Subjective Conflict Evaluation

In line with previous evidence that suggests that emotion and executive functions share neural processes [Ochsner et al., 2012; Okon-Singer et al., 2013, 2014, 2015; Rohr et al., 2015], our conjunction analysis found STS and IPL to be involved in both the prioritization of either positive or negative cues and subjective conflict evaluation. Greater activity in the STS correlated with subjectively evaluating a conflict as less intense, and also correlated with prioritizing positive over negative cues during the scenes. Greater activity in the IPL, in contrast, correlated with subjectively

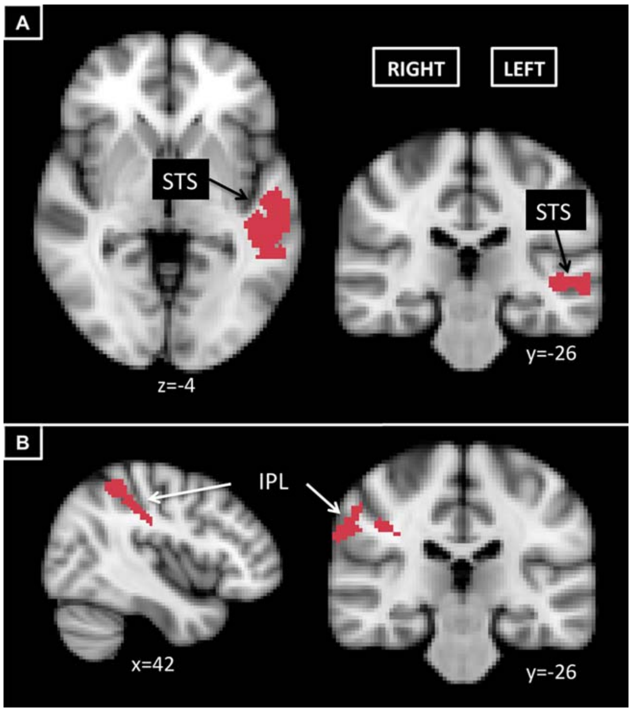

Figure 4.
Conjunction map of the results for conflict evaluation and valence prioritization. (A) Functional activity in left STS was negatively correlated with subjective conflict evaluation, and greater when positive cues were prioritized over negative ones. (B) Neural activity in the right IPL was positively correlated with subjective conflict evaluation, and greater when negative cues were prioritized over positive ones. IPL = supramarginal gyrus/inferior parietal lobule; STS = superior temporal sulcus. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

evaluating the conflict as more intense, and also correlated with prioritizing negative over positive cues during the scenes. Therefore, STS and IPL may be important in processes that are shared by subjective conflict evaluation and valence prioritization and may even constitute "hubs" or "switches" in socio-emotional conflict processing, involved in "resolving" the conflict by helping to make decisions on which valence should be given preference. The identification of such a mechanism might have implications for recent discussions on emotional traits and the cognitive control of emotion, given that people who score high on extraversion and positive affect are thought to give preference to positive cues, while people who score high on neuroticism and negative affect are known to give preference to negative cues in ambiguous situations [Burger, 2010]. Both STS and IPL have previously been implicated in the cognitive control of emotion [Ochsner et al., 2012], and both the increase of negative attitude in depressed patients and bias toward threat-related stimuli in patients with anxiety have been proposed to modulate the neural networks associated with emotional conflict processing [Fales et al., 2008; Haas et al., 2007; Mitterschiffthaler et al., 2008]. STS is thought to be vital in understanding the intentions of other people [Allison et al., 2000], and to be specifically involved in representing social cues to emotion like movements of lips and eyes [Allison et al., 2000; Brefczynski-Lewis et al., 2011; Wheaton et al., 2004]. Therefore, STS activity may indicate better social understanding of a given situation, which in turn may decrease the subjective perception of conflict between presented cues. STS has also been linked to reappraisal during the cognitive control of emotion and emotional conflict processing [Kanske et al., 2011; McRae et al., 2010]. Kotz et al. [2015] found that STS was more active when participants listened to incongruent sentences that contained a positive intonation (alongside negative semantic content) when compared with congruent positive sentences. IPL has been attributed with a role in selective attention, working memory [Miller, 2000; Wager and Smith, 2003; Wager et al., 2004] and error-detection [Garavan et al., 2003; Hester et al., 2004; Ullsperger and von Cramon, 2001, 2004]. Zaki et al. [2010] found that IPL was more active when participants gave preference to a verbal description rather than a facial expression when both were presented simultaneously in an incongruent way. Thus, there may be a relationship between activity in the STS and more automatic and effortless processing, which leads to prioritization of positive cues, and between activity in the IPL and more conscious and exertive processing, which leads to prioritization of negative cues, within socio-emotionally conflicting settings.

Our contrast analysis of prioritization of positive or negative cues further revealed additional regions previously related to emotional conflict that became more active alongside STS and IPL. During prioritization of positive

TABLE III. Increases in functional connectivity during prioritization of positive over negative cues

Lat	Seed	Lat	Connectivity	BA	Voxels	*P*-Value	*Z*-Max	*x*	*y*	*z*
L	STS	BIL	PCC-Precuneus	23, 31, 7	11,517	<0.000001	4.2	4	−30	48
		BIL	d-rmPFC, d-rACC	8-10, 24, 32, 33						
		R	IPL	39, 40	920	0.000531	3.21	34	−48	38
		BIL	Thalamus, Caudate	-	633	0.00765	3.53	−4	4	2

BA = Brodmann Area; d-rACC = dorsal-rostral Anterior Cingulate Cortex; d-rmPFC = dorsal-rostral medial Prefrontal Cortex; IPL = Inferior Parietal Lobule; PCC = Posterior Cingulate Cortex; STS = Superior Temporal Sulcus.

TABLE IV. Increases in functional connectivity during prioritization of negative over positive cues

Lat	Seed	Lat	Connectivity	BA	Voxels	*P*-Value	Z-Max	*x*	*y*	*z*
R	IPL	BIL	FuG, LG, OP	37, 19, 17, 18	1,5010	<0.000001	4.85	24	−76	−10
			Cuneus, PCC, IPL	19, 23, 31, 39, 40						
		BIL	vmPFC, vACC	10, 24	2,446	<0.000001	4.07	6	34	22

BA = Brodmann Area; FuG = Fusiform Gyrus; IPL= Inferior Parietal Lobule; LG = Lingual Gyrus; OP = Occipital Pole; PCC = Posterior Cingulate Cortex; vACC = ventral Anterior Cingulate Cortex; vmPFC = ventromedial Prefrontal Cortex.

cues, enhanced activity was found in dmPFC and a region in posterior amygdala and anterior hippocampus, while during prioritization of negative cues, the insula was more active. These findings point to the possibility that the involvement of amygdala and dmPFC in emotional conflict may be influenced by processes involved in the generation of valence prioritization. This is in line with studies that link the amygdala to the perception and encoding of stimuli relevant to short- or long-term affective goals [Cunningham et al., 2008, 2011; Davis and Whalen, 2001; Hariri and Whalen, 2011; Okon-Singer et al., 2013; Phelps, 2006] and implicate dmPFC in making judgments about mental states [Mitchell, 2009; Zaki and Ochsner, 2011; Zaki et al., 2012].

STS, IPL, insula and mPFC are considered to be part of a network crucial for social cognition and theory of mind, which subserves making inferences about the mental states of others, alongside PCC, precuneus and FuG [Mar, 2011; Wolf et al., 2010; Zaki et al., 2010]. The enhanced connectivity between these regions found in our PPI analyses is in line with the idea that making inferences about the mental states of others can be regarded as an important feature of socio-emotional conflict processing (consider, e.g., the task of correctly decoding what the person with the happy facial expression but the negative verbal information intends to communicate) [also see Kotz et al., 2015; Zaki et al., 2010]. Our findings also link to a recently developed framework which draws parallels between cue integration in social cognition and physical perception, and relies heavily on the aforementioned regions [Zaki, 2013]. This framework assumes that conditional probabilities exist for conflicting cues one way or another depending on individual evaluations of sensorimotor versus contextual cues, and the estimated likelihood of them being reliable. For example, in our study, while watching the scene from "Reservoir Dogs," a participant could infer that sensorimotor cues are reliable ("I know the gangster is holding the cop hostage, but he's dancing and smiling, so surely he won't harm him"), or they may deem contextual information to be more reliable ("The gangster may appear charming, but he's holding a sharp razor in his hands"). Within the conceptualization of this framework, sensorimotor cues are processed by an "experience sharing" network including STS, IPL, insula and ACC, while contextualizing cues are processed by a "mentalizing" network including mPFC, precuneus and PCC [please see Zaki, 2013 for details]. Our current findings indicate that these networks functionally interlink during emotional conflict processing. During prioritization of positive over negative cues within the scenes, left STS had significantly increased connectivity with bilateral dorsal-rostral mPFC and dorsal-rostral ACC, as well as PCC and precuneus. Enhanced functional connectivity between the STS and these regions was recently associated with higher empathizing [Takeuchi et al., 2014], which is much in line with the notion of identifying mental states of others. During prioritization of negative over

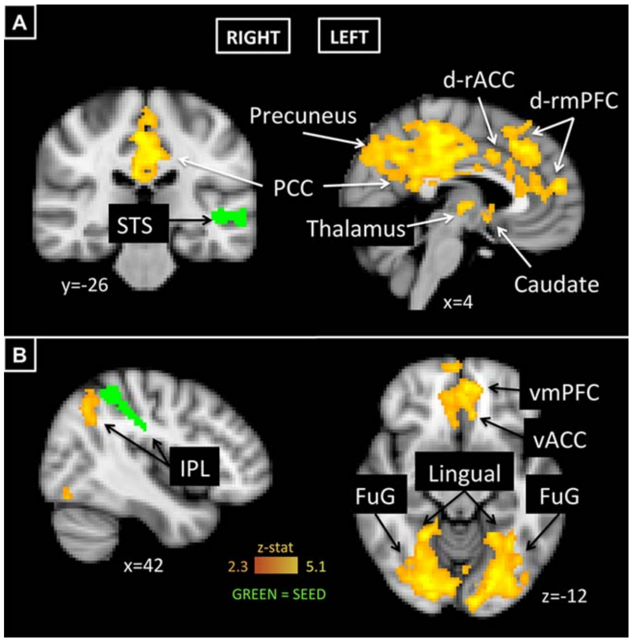

Figure 5.

Increases in functional connectivity during prioritization of (A) positive over negative and (B) negative over positive cues. d-rACC = dorsal-rostral anterior cingulate cortex; d-rmPFC = dorsal-rostral medial prefrontal cortex; FuG = fusiform gyrus; PCC = posterior cingulate cortex; IPL = inferior parietal lobule; STS = superior temporal sulcus; vACC = ventral anterior cingulate cortex; vmPFC = ventromedial prefrontal cortex. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

positive cues, right IPL had significantly increased connectivity with ventral mPFC, ventral ACC and FuG. IPL, mPFC and ACC have been shown to coactivate in response to facial expressions of pain [Budell et al., 2010]. Right IPL also had significantly increased connectivity with FuG and LG bilaterally. We previously found that stronger connectivity between these regions predicted higher trait negative affect [Rohr et al., 2013], which further supports the notion that valence prioritization within emotional conflict may be related to emotional traits (see above).

Limitations and Future Directions

The findings of the present study are limited to the descriptive scope of the employed measures. In this study, our focus was to examine valence prioritization within subjectively evaluated emotional conflicts. In order to keep the design as intuitive as possible, we collected continuous ratings along a positive-negative spectrum while measuring conflict across the scenes as an average. In future studies, it will be interesting to also (a) collect continuous ratings of conflict, as perceived conflict levels may fluctuate during the experience, and (b) to separate the valence spectrum into a positive and a negative scale, in order to allow for more detailed assessments of the relationship between the evaluation of conflict and the prioritization of valence, and their neural correlates. While films are known to elicit strong emotions and are life-like in the sense that they contain moving images and sounds, there is still a difference between the neural response to a film and a real situation. Fictional characters and stories, for one, can be extreme versions of their everyday counterparts: protagonists are heroes without fault, while antagonists are psychopathic villains. Conflicts in real life, moreover, can directly involve us and require us to react, whereas conflicts in films involve us indirectly when we identify with the characters and become immersed in the story. Future studies using interactive designs may therefore add valuable insights into emotional conflict processing when a person is directly involved. The scenes that we used here to elicit emotional conflict were taken from Hollywood films within four genres (Drama, Thriller, Horror and Crime). Given that movies elicit a whole range of emotions that are hard to disentangle, future research may test whether our findings generalize to other genres and independent films. While our study, like several studies before [Hutcherson et al., 2005; Nummenmaa et al., 2012; Raz et al., 2012], relied on the use of individual ratings and was not designed to run contrasts between conflicting and neutral film scenes, or conflicting and nonconflicting film scenes, such investigations may allow for further inferences to be drawn about the roles of IPL, STS, PFC and amygdala in subjective evaluations of conflict, valence prioritization, and other variables of interest in regard to complex conflict processing.

Conclusions

Our data propose a role for IPL and STS in the subjective evaluation of complex conflicts, as well as in the prioritization of either positive or negative cues. Thus, these regions may constitute "hubs" or "switches" in socioemotional conflict processing. Amygdala and prefrontal regions—regions implicated in emotional conflict tasks which require a predefined distracter that conflicts with a target to be ignored—were involved in valence prioritization in the present study, but not subjective evaluation of conflict. Indicative of a potential pathway, IPL and STS were differentially connected to prefrontal control centers during valence prioritization. Connectivity patterns further implicated PCC, precuneus and FuG in valence prioritization, highlighting the importance of regions within the social cognition and theory of mind networks for socioemotional conflict processing.

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