Controlling Emotional Expression: Behavioral and Neural Correlates of Nonimitative Emotional Responses

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Emotional facial expressions can engender similar expressions in others. However, adaptive social and motivational behavior can require individuals to suppress, conceal, or override prepotent imitative responses. We predicted, in line with a theory of "emotion contagion," that when viewing a facial expression, expressing a different emotion would manifest as behavioral conflict and interference. We employed facial electromyography (EMG) and functional magnetic resonance imaging (fMRI) to investigate brain activity related to this emotion expression interference (EEI) effect, where the expressed response was either concordant or discordant with the observed emotion. The Simon task was included as a nonemotional comparison for the fMRI study. Facilitation and interference effects were observed in the latency of facial EMG responses. Neuroimaging revealed activation of distributed brain regions including anterior right inferior frontal gyrus (brain area [BA] 47), supplementary motor area (facial area), posterior superior temporal sulcus (STS), and right anterior insula during emotion expression–associated interference. In contrast, nonemotional response conflict (Simon task) engaged a distinct frontostriatal network. Individual differences in empathy and emotion regulatory tendency predicted the magnitude of EEI-evoked regional activity with BA 47 and STS. Our findings point to these regions as providing a putative neural substrate underpinning a crucial adaptive aspect of social/emotional behavior.

Keywords: emotion, facial expression, functional magnetic resonance imaging (fMRI), interference

Introduction

The ability to inhibit and correct prepotent responses is a central feature of executive function, enabling the adaptive control of behavior beyond immediate stereotyped responses and reactions. The development of response control and associated behavioral flexibility, evident in phylogenetic evolution and in human maturation, suggests that it mediates behavioral advantages. Within experimental psychology, response control is typically examined using facilitation/interference paradigms. Congruence of behavioral cue with a prepotent response is facilitatory, reflected typically as a reduction of reaction times (RTs). Conversely, overcoming prepotent psychological or behavioral tendency to execute an alternative intended response is manifested as a "cost," reflected experimentally in prolonged RTs.

Behavioral interference tasks have explored a variety of contexts: the most widely known is the Stroop Color–Word Task (Review; MacLeod 1991). In the Stroop task, subjects view words describing different colors (e.g., blue, red, etc.) and are required to name the color of the ink in which the words are printed. Ink color and response may be congruent (e.g., the word blue printed in blue ink) or incongruent (blue printed in red ink). The interference effect on incongruent trials reflects a cost in suppressing the prepotent response to read the color word. Interference in other aspects of cognition (e.g., counting Stroop; Bush et al. 1998; Hayward et al. 2004) and emotion processing (e.g., emotional Stroop; Bentall and Thompson 1990; Williams et al. 1996; Compton et al. 2003; Malhi et al. 2005) has been explored using Stroop-like conflict tasks. Moreover, because behavioral conflict is typically expressed at the level of response, a number of studies have focused on competition within spatial and motor response dimensions (e.g., Simon task; Fitts and Deininger 1954; Maclin et al. 2001). Nevertheless, although interference effects are observable across perceptual, cognitive, emotional, and motoric domains, it remains unclear whether a common neural mechanism mediates an ability to override prepotent responses. Indeed, there is evidence for both common (Peterson et al. 2002) and dissociable (Whalen et al. 1998) neural substrates mediating response competition.

In the present study, we extended Stroop effect to the underexplored dimension of emotion expression interference (EEI). The ability to control and contain our evoked emotional responses is important for adaptive emotional behavior (Gross 1998). Emotional facial expressions represent potent social cues and empirical evidence suggests that emotions and facial expressions are "contagious." Thus, in facial electromyographical (EMG) studies, viewing smiling and frowning faces implicitly activate corresponding "zygomaticus major muscle" and "corrugator muscle," respectively, in the viewer (Dimberg 1982; Dimberg et al. 2002). We hypothesized that this mimicry tendency (with "resonant" patterns of neural activity; Lee et al. 2006) represents a prepotent response bias that would interfere with the ability to express a different opposite facial emotion (frowning to smiling faces or vice versa).

First, we performed a facial EMG study, where the subjects viewed video clips depicting happy or angry emotional expressions while directed to express a concordant or discordant facial emotion (i.e., smile or frown). Second, following the EMG study (which validated the presence of an interference effect), we applied functional magnetic resonance imaging (fMRI) to delineate brain regions responsible for this EEI effect. We predicted that EEI would require extra expressive and inhibitory effort, reflected in enhanced activity within motor-related region and inferior frontal cortex (Carr et al. 2003; Leslie et al. 2004; Lee et al. 2006). Moreover, inhibition of prepotent emotional expressions EEI is likely to be facilitated by enhanced self-generated representation of the appropriate (intended) emotional feeling states (e.g., by recruiting activity within

regions such as right anterior insula cortex; Reiman et al. 1997; Critchley et al. 2004). Lastly, to examine stimulus–response (S–R) compatibility (conceptually distinct from stimulus–stimulus compatibility; Fitts and Deininger 1954; Simon and Berbaum 1990) in affective and nonaffective contexts, we also included a modified Simon task to serve as a nonemotional comparison of the interference effect (Valle-Inclan 1996; Wascher et al. 1996).

Materials and Methods

Subjects, Experimental Stimuli and Questionnaires

We recruited 32 volunteers for the EMG study (mean age, 22.7 years; 14 males [M], 18 females [F]) and 14 among them for the fMRI study (mean age, 23.8 years; 7 M, 7 F). Each gave informed written consent approved by the local Ethics Committee. Subjects were screened to exclude history or evidence of neurological, medical, or psychological disorder including substance misuse. None of the subjects was taking medication.

Experimental stimuli consisted of 700 ms video clips of 2 dynamic facial expressions portraying anger and happiness from 10 M and 10 F models. Each movie was further processed by SmartMorph (http://meesoft.logicnet.dk/SmartMorph/) to create 4 different intensities of emotional expression: 25%, 50%, 75%, and 100%. These 4 intensities provided a stimulus platform for the subject to make subjective emotion intensity judgments (Fig. 1*i*). In total, we constructed 160 different movies from 20 different identities.

We administered 2 questionnaires to subjects to probe the relationship between EEI effects and 2 related dimensions, namely: Empathy Quotient (EQ) and Emotion Regulation Questionnaire (ERQ; Gross and John 2003; Lawrence et al. 2004). EQ comprises 3 subscales: "cognitive empathy," "emotion reactivity" (close to the concept of emotion empathy), and "social skills." ERQ includes subscales of "reappraisal"
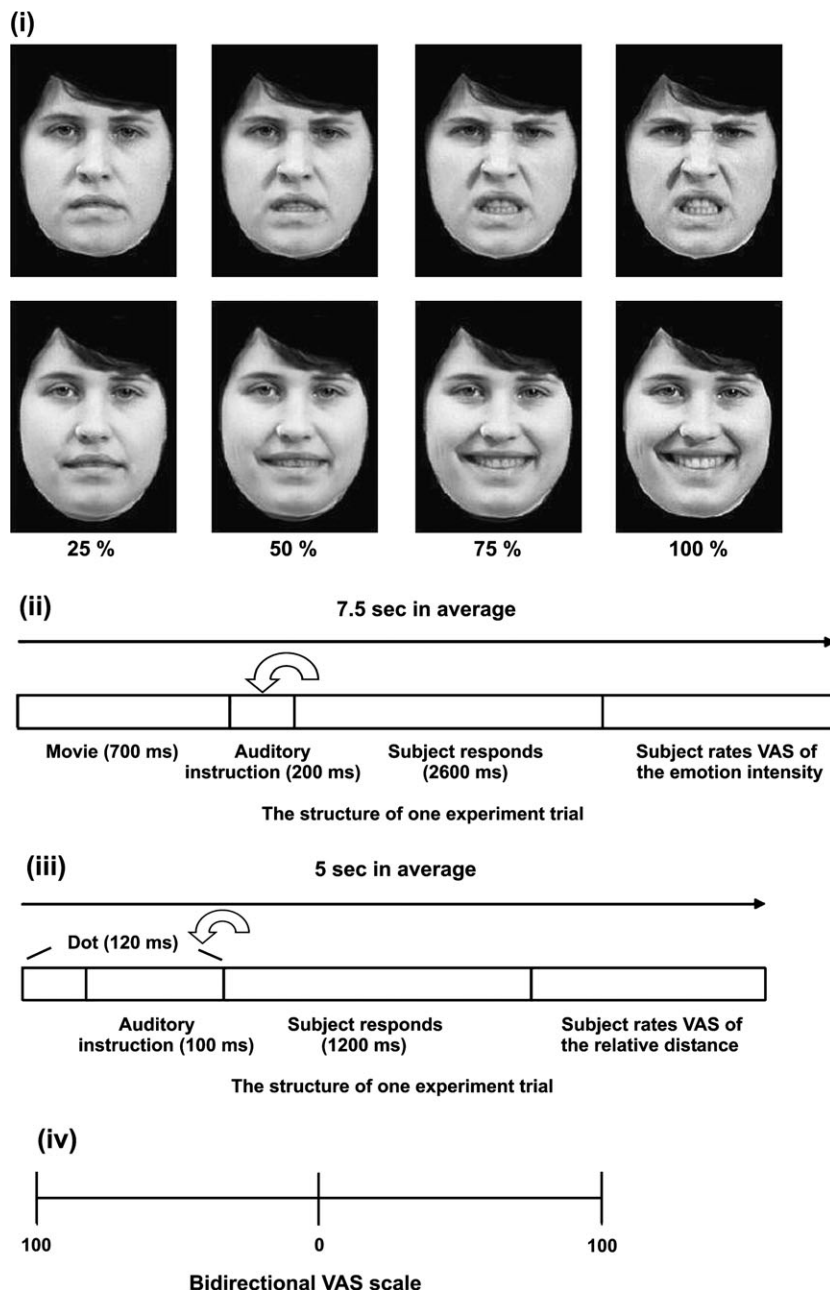
Figure 1. Examples of experimental stimuli (*i*) and the structure of a single trial for EEI task (*ii*) and Simon task (*iii*). The VAS used is illustrated in (*iv*).

and "suppression." Because the central themes of EEI involve the relationship between contagiousness of emotion expression (emotion empathy) with expressive control (suppression), we were particularly interested in the emotion reactivity subscale of the Empathy Quotient (EQ-er) and suppression subscale of the Emotion Regulation Questionnaire (ERQ-supp).

EEI Task
The experimental EEI task was identical in both the EMG and fMRI studies and comprised of 2 sessions, each with 160 trials. On each trial, the subject viewed a movie clip depicting a different intensity of happy or angry expression. At the end of each movie, the subject was required to either frown or smile in response to 200 ms auditory cue. The subject was instructed before the task to respond as quickly as possible (to enhance the automaticity of interference effects). The auditory instruction was concordant or discordant with the expression in the movie, resulting in both congruent and incongruent trials; that is, smiling to happy faces (SS), smiling to angry faces (SF), frowning to happy faces (FS), and frowning to angry faces (FF). Subjects performed an emotion intensity judgment (visual analog scale [VAS]) 2.6 s after the offset of the auditory instruction. Responses were made using a monitor display and a 2-button, hand-held response pad (Fig. 1*iv*). Intertrial intervals were varied from 6.5 to 8.5 s to reduce anticipatory effects (Fig. 1*ii*). Because each of the 160 movies could be followed by 2 different instructions, frown or smile, there were a total of 320 audiovisual trial stimuli, each presented just once to the subjects. The trial sequence was fully randomized.

EMG Study

EMG Recording
In the EMG study, subjects performed the EEI task while we recorded facial EMG via BioSemi system (www.biosemi.com) in a shielded room. To register movement responses, 2 pairs of bipolar surface electrodes were attached on the left side of the subject's face, consistent with studies reporting more extensive left hemiface movement during emotional expression (Rinn 1984). The regional locations corresponded to optimal recording sites for the EMG activities of "corrugator supercilii" and "zygomaticus major." The former reflects frowning and the latter smiling. Ground electrodes were positioned below the hairline of forehead. Electrode placement followed standard facial EMG guidelines (Fridlund and Cacioppo 1986) with interelectrode distance 1 cm. Sample rate was set at 2048 Hz.

EMG Data Analysis
EMG data were band-pass filtered between 10 and 500 Hz and full-wave rectified. The data were smoothed using a root mean square analysis with 60 ms window. An 8-s epoch was segmented for each experimental trial (from 1 s before the commencement of each movie). Onset latency was defined by more than 3 standard deviations (SDs) above the baseline level (average of the 100 ms before the commencement of the trial) for a minimum of 50 ms.

Outlying data (rejected trials) were defined as trials where averaged latency exceeded 3 SDs away from the mean, where EMG activity onset occurred before the auditory instruction or rating of opposite emotion. The filtered and smoothed EMG data were visually checked to verify the automatically identified onsets, missing responses, and the rejected trials.

fMRI Study

EEI and Simon Task
A random subset ($N = 14$) subjects of the EMG subjects took part in the fMRI study. Each subject performed the EEI task over 2 sessions, with 256 trials in total, in an identical manner to the facial EMG study. In a third session, the subjects performed a nonemotional interference task; a modified Simon task with similar design structure to the emotion expression (EEI) task. This task served as a comparison for nonemotional interference effects. In this task, the subject was required to fixate on a central cross, which was constantly displayed on the screen. An auditory instruction (100 ms; the content was "left" or "right") 20 ms

came after the visual presentation of a white dot (120 ms duration) at a location either the left or the right of the central fixation cross. The distance of the white dot was variable; ranging from 25% to 90% of the half-width of monitor. This variability in distance embodied the parametric properties of facial stimuli in the earlier EEI task. The subject was requested to press the left or right button as quickly as possible according to the auditory instruction. Thus, the subject's response was either to the same (concordant) or opposite (discordant) position relative to the viewed dot. After responding, the subject rated the perceived distance of the dot from the central cross on a VAS, 1.2 s after the offset of the auditory instruction (Fig. 1*iii,iv*). Trial length ranged from 4 to 6 s and (mean 5 s). There were 128 trials in total, and the trial sequence was randomized. Thus, the Simon task design shared with the emotion judgment (EEI) task the following requirements: the subject 1) passively viewed stimuli with different parametric attributes; 2) made a rapid forced-choice response to an auditory instruction, in a manner either concordant or discordant with the visual stimuli; and 3) referred to an internal/invisible standard.

Before fMRI scanning, all the subjects received 15 min of training in both tasks. During training, correct response rates for both the emotion (EEI) and the modified Simon task were higher than 95% (a video camera was used to record responses to confirm performance accuracy in the emotion expression task).

fMRI Data Acquisition
We acquired sequential T_2*-weighted echoplanar images (Siemens Allegra, Erlangen, Germany, 3-T, 44 slices, 2.0 mm thick, time echo 0.65 ms, time repetition 2.86 s, voxel size $3 \times 3 \times 3$ mm³) for blood oxygenation level–dependent (BOLD) contrast. The slices covered the whole brain in an oblique orientation of 30 degree to the anterior–posterior commissural line to optimize sensitivity to orbitofrontal cortex and medial temporal lobes (Deichmann et al. 2003). Head movement was minimized during scanning by comfortable external head restraint. Three hundred and twenty whole-brain images were obtained over 16 min for the 2 emotion sessions and 240 images over 12 min for the Simon session. The first 5 echoplanar volumes of each session were not analyzed to allow for signal equilibration effects. A T_1-weighted structural image was obtained for each subject to facilitate anatomical description of individual functional activity after coregistration with fMRI data.

fMRI Data Analysis
We used SPM2 analysis software (http://www.fil.ion.ucl.ac.uk/spm/spm2.html) on a Matlab platform (Mathworks, Inc., Natick, MA) to analyze acquired fMRI data. Scans were realigned (motion corrected), unwarped, spatially transformed to standard stereotaxic space (with respect to the Montreal Neurologic Institute coordinate system) and smoothed (Gaussian kernel full-width half-maximum, 8 mm) prior to analysis. Task-related brain activities were identified within the general linear model.

In individual subject analyses, low-frequency drifts and serial correlations in the fMRI time series were respectively accounted for using a high-pass filter (constructed by discrete cosine basis functions) and nonsphericity correction, created by modeling a first degree autoregressive process (http://www.fil.ion.ucl.ac.uk/spm/; Friston et al. 2002). Error responses were defined as the trials in which a subject misclassified the video clips/dots (i.e., where happy movie were rated as angry) or pressed the button opposite to the auditory instruction in the Simon task. Errors were modeled within the design matrix. For the emotion (EEI) task, activity related to stimulus events was modeled separately for the 4 different categories (SS, SF, FS, FF) using a canonical hemodynamic response function (HRF) with temporal and spatial dispersion derivatives (to compensate for discrepant characteristics of hemodynamic responses). To test whether the averaged interference brain map revealed parallel results in the high and low interference conditions, another analysis was performed by dividing the experimental trials into high and low interference groups according to highest and lowest 20% rated emotion intensity. In the analysis of the Simon task, we modeled the concordant and discordant conditions with the same 3 hemodynamic basis functions in a similar statistical model to the EEI task analysis for comparison. Additionally, individual correlational maps for concordant and discordant conditions were constructed voxel-by-voxel from the correlation coefficient of linearly detrended measured BOLD

effects and acquired emotion intensity ratings of the stimuli (aligned in time and convolved with a canonical HRF). Contrast images for interference effects ([SF + FS – SS – FF] for the EEI task and [discordant–concordant] for Simon task) and the 2 correlation maps (discordant and concordant) were entered into group level (second-level) analyses using an analysis of variance model.

The second-level group analyses (random effects with nonsphericity correction) were explored separately using F-tests of event-related activity reflecting interference in the EEI and Simon tasks. Voxel-wise statistical threshold was set at $P < 0.001$, uncorrected. To constrain our analysis to brain regions specific to EEI processing, we used an exclusive mask derived from Simon task. A "discordant minus concordant" t-test was used in the analysis of the correlation maps to explore the brain regions showing parametric EEI.

Results

EMG Study

Inspection of individual data revealed a parametric relationship between the latency of EMG response onset and the viewed and rated perceived intensity of emotion in both frowning and smiling conditions. This significant trend was most prominent when combining concordant and discordant conditions (illustrated in Fig. 2). Thus, EMG onset latency decreased with increasing emotion intensity in the concordant conditions (frowning to frowning faces, smiling to smiling faces) and increased with increasing emotion intensity in the discordant conditions (frowning to smiling faces, smiling to frowning faces). Across subjects, the average correlation coefficients of EMG onset latency and rated emotion intensity were: 0.3165 for frowning condition (SD = 0.155, $P < 0.001$, degree of freedom [df] = 31) and –0.3998 for smiling condition (SD = 0.154, $P < 0.001$, df = 31).

In response to the stimuli depicting frowning, mean EMG onset latency for concordant responses was 364.2 ms (SD = 93.1) and for discordant responses was 452.3 ms (SD = 103.7). Similarly, in response to smiling stimuli, mean EMG onset latency for concordant responses was 325.8 ms (SD = 97.5) and for discordant responses was 444.3 ms (SD = 133.7). To highlight this congruency effect, we took the extreme 20% (each of smiling and frowning) stimuli with the strongest emotion intensity ratings and the 20% of trial stimuli with the lowest emotion intensity ratings (rating around zero) for concordant and discordant trials and analyzed the difference in average EMG onset latency. The 4 paired-samples t-tests all reached statistical significance with P values less than 0.001, verifying both interference and facilitation effects; see Table 1. The average error rate on the EEI task was 7.5% comprising missing/wrong responses, contamination of baseline due to early muscle activities or blinks, and rating of opposite emotion valence. The error responses were excluded from the analysis.

We also explored the relationship between EMG latency and interindividual differences in emotional style (EQ). Across subjects, the EQ-er correlated significantly with EMG onset in concordant condition, with correlation coefficient –0.415 for frowning ($P = 0.018$) and 0.476 for smiling ($P = 0.006$) but not in discordant condition, with correlation coefficient –0.294 for frowning ($P = 0.102$) and 0.128 for smiling condition ($P = 0.484$).

fMRI Study

For the emotion (EEI) task, mean intensity ratings across subjects for the angry movies was 38.1 (SD = 10.8) and for the happy movies 38.2 (SD = 8.4). There was no significant

difference between these ratings. No gender differences were observed between subjects in the rating of stimulus intensity.

In the Simon task, mean RTs for concordant and discordant conditions were 445.7 and 509.8 ms, respectively ($P < 0.001$, $t = 5.162$, df = 13). In contrast to behavioral results of the EEI study, correlations between stimulus dot position and motor RT in the Simon task did not reach statistical significance. The average response error rate across subjects was 9%.

Brain Activity Relating to EEI

Brain regions demonstrating significant differential activity during EEI (incongruent vs. congruent responses) included motor cortex, ventrolateral prefrontal cortex, lingual gyrus, and right anterior insula (see Fig. 3 and Table 2 for detail). The high and low interference maps of EEI generally coincided with the averaged interference map. Interestingly, significant activity changes within genual or dorsal anterior cingulate cortex (dACC) were not evoked by EEI. Because of the difficulty implementing accurate facial EMG within the 3-T magnetic resonance imaging environment, we could neither identify all error responses in EEI nor provide brain activation map of error responses in EEI. However, participants were overtrained in the task before scanning, where performance exceeded 95%, and during scanning, the error rate of EEI score (i.e., misassigning positive emotions as negative and vice versa) was 1.3%.

Brain Activity Relating to Interference Effect of Simon Task

The Simon task provided a nonemotional comparison for our EEI task. Conflict and interference during the Simon task evoked changes in frontostriatal activity. Modulation of activity within visual association cortices, left posterior insula, and cerebellum was also observed (Fig. 4 and Table 3). Taking the SPM of Simon task as an exclusive mask (even under a generous statistical threshold, uncorrected $P < 0.01$, see below), the EEI SPM remains unchanged, suggesting limited overlap in the neural substrates for overcoming emotional and nonemotional response conflicts. No response interference effect was observed in dACC during the Simon task, yet, strikingly, error responses caused robust dACC activation (uncorrected $P < 0.001$) (Fig. 4).

Brain Correlation Map

We predicted that interference (EEI) effects would be amplified by increases in perceived emotion intensity of the viewed facial stimuli. To test this, we constructed brain correlation maps of EEI (by correlating brain activity and subjective rating, see Materials and Methods) and calculated the contrast of discordant and concordant conditions. As with the categorical EEI analysis, activity within inferior frontal gyrus (IFG) (brain area [BA] 47), right anterior insula, and superior temporal sulcus (STS) was modulated during EEI, as a function of the perceived emotional intensity of the facial expressions. In addition, bilateral middle frontal gyri and left orbitofrontal gyrus also demonstrated this parametric aspect of conflict in emotional expression (Table 4). As to the Simon task because the dot position did not modulate the interference effect, further correlation analyses were not performed.

Within our second-level analyses, we also explored the predictive relationship between activity during EEI (in right anterior insula, right IFG, and bilateral STS) and interindividual differences in emotional style (EQ, ERQ). Across subjects, the EQ-er correlated significantly with activity within left STS ($P = 0.007$). Similarly, the suppression subscale of ERQ (ERQ-supp) correlated with EEI-related activity within right IFG
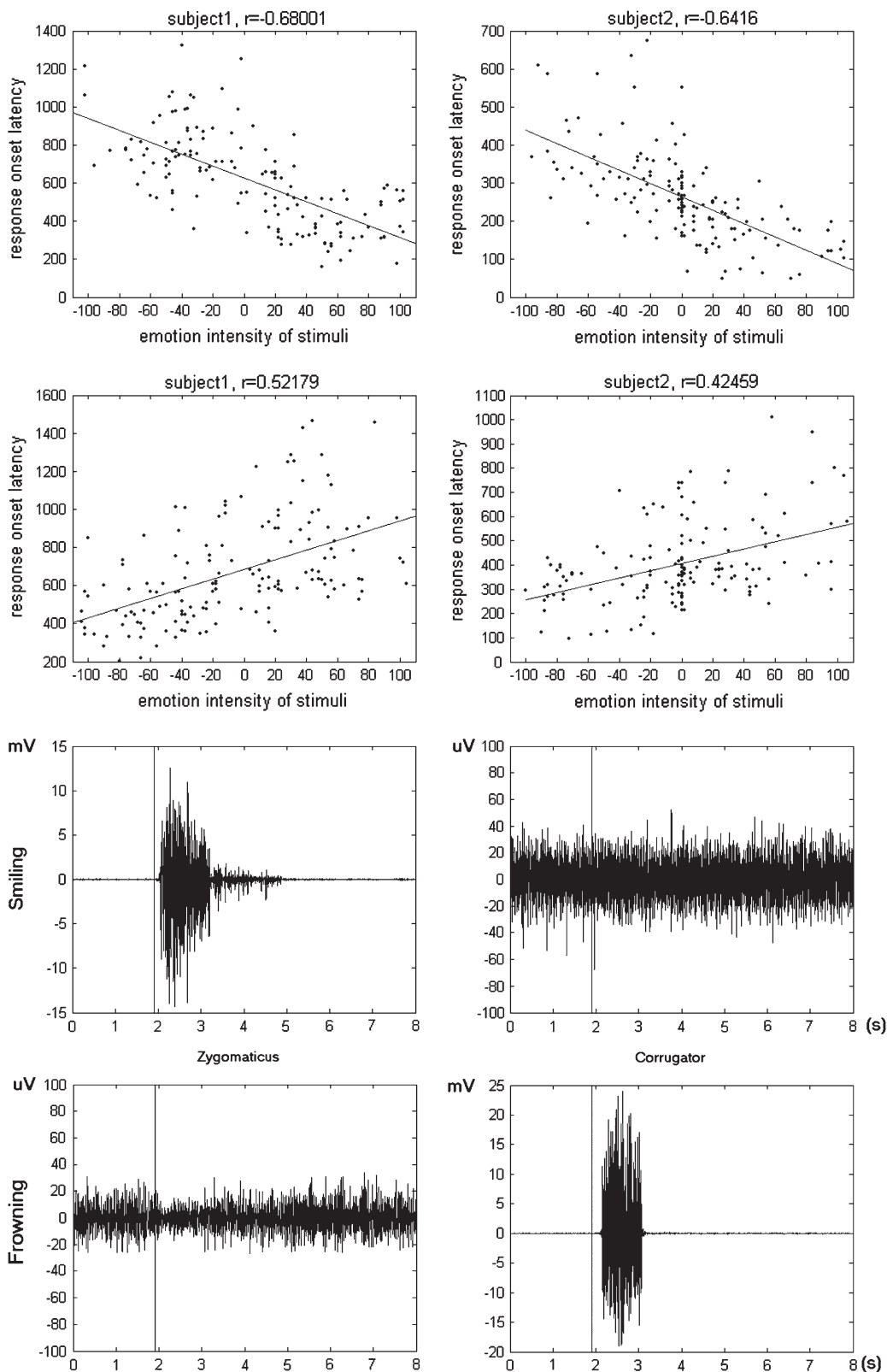
Figure 2. The relationship between emotion intensity and EMG response onset. Upper: The ordinate is the EMG onset latency (ms), and the abscissa is the rating of emotion intensity. Positive and negative values indicate the degree of anger and happiness rated by the subjects. The relationship between EMG onset and perceived emotion intensity was illustrated for 2 randomly selected subjects, with the 1st row for zygomaticus and 2nd row for corrugator muscle. The P values of the correlation coefficient are all below 0.001. Lower: The filtered facial EMG response of smiling and frowning at zygomaticus and corrugator muscle. The vertical line marks the offset of audiovisual stimulus.

($P = 0.017$). These rating and correlation results are summarized in Table 5.

Discussion

This study explored a novel Stroop-like effect, namely, EEI. This interference effect highlights automatic emotional conflict at the level of S–R compatibility. In our behavioral facial EMG study, we showed facilitation and interference effects on emotional expression from RTs. Besides, the EMG onset in concordant condition correlated negatively with the personal emotion reaction, reflected in the EQ-er (EQ-er reflects the tendency to react emotionally to the emotions of others; Lawrence et al. 2004), implying that people with higher emotional empathy respond faster to others' facial expressions. In our neuroimaging study, we show that EEI is mediated by an emotion-related sensorimotor network that includes bilateral STS, right anterior insula, right IFG, and supplementary motor area (SMA). This neural activation pattern differs from observations in classical Stroop/interference paradigms. Notably, within our experimental subjects, this profile did not overlap with interference-related activity engendered by the Simon task. We also illustrated that conflict-related neural activity within IFG, right anterior insula, and STS was directly sensitive to the perceived intensity of emotional expression stimuli, further endorsing the role of these regions in EEI at the level of S–R conflict.

It is highly possible that the EEI originates at the level of mimicry, requiring an individual to overcome the intrinsic imitative tendency evoked by the emotional facial expression of another. The underlying mechanism for this "emotion contagion" effect, highlighted by a series of EMG studies (Dimberg 1982), is still under debate. Measurement of the mimicry tendency at response level does not necessarily mean that it goes through motoric mimicry. For example, specific facial EMG pattern can also be aroused to nonface emotional stimuli (Dimberg 1986). Various social or emotional behaviors automatically become active in the presence of relevant behavior or stereotyped-group features (Bargh et al. 1996). Further, the automatic mimicry is shaped by personal characteristics (Sonnby-Borgstrom 2002). These observations point to heterogeneous pathways underlying mimicry tendency that are not exclusive to each other. In other words, the emotion contagion may work through emotional, motoric, cognitive evaluative channels, or in combination. Our previous study of imitating emotional facial expressions highlighted the involvement of both motoric and emotional (notably amygdala) centers (Lee et al. 2006). EEI is likely to engage both emotional and motoric pathways.

Table 1
The mean EMG onset latency of frowning and smiling while viewing movies carrying different emotions

Responses	Movies	Mean (ms)	SD	t	df	P value
Frown	Angry[a]	335.6	93.9			
	Happy[a]	455.2	105.1			
	Neutral[b]	425.2	101.0			
Smile	Angry[a]	449.8	129.1			
	Happy[a]	289.9	96.5			
	Neutral[b]	403.1	124.6			
Paired differences						
Frown	Angry–neutral	−89.6	60.5	−8.376	31	<0.001
	Happy–neutral	30.0	42.5	3.994	31	<0.001
Smile	Angry–neutral	46.7	56.9	4.640	31	<0.001
	Happy–neutral	−113.2	66.6	−9.614	31	<0.001

Note: Paired difference analysis was based on the above 40% data points.
[a]Twenty percent samples with strongest emotion rating was included in the analysis.
[b]Twenty percent samples with lowest emotion rating (rating around zero) was included in the analysis.
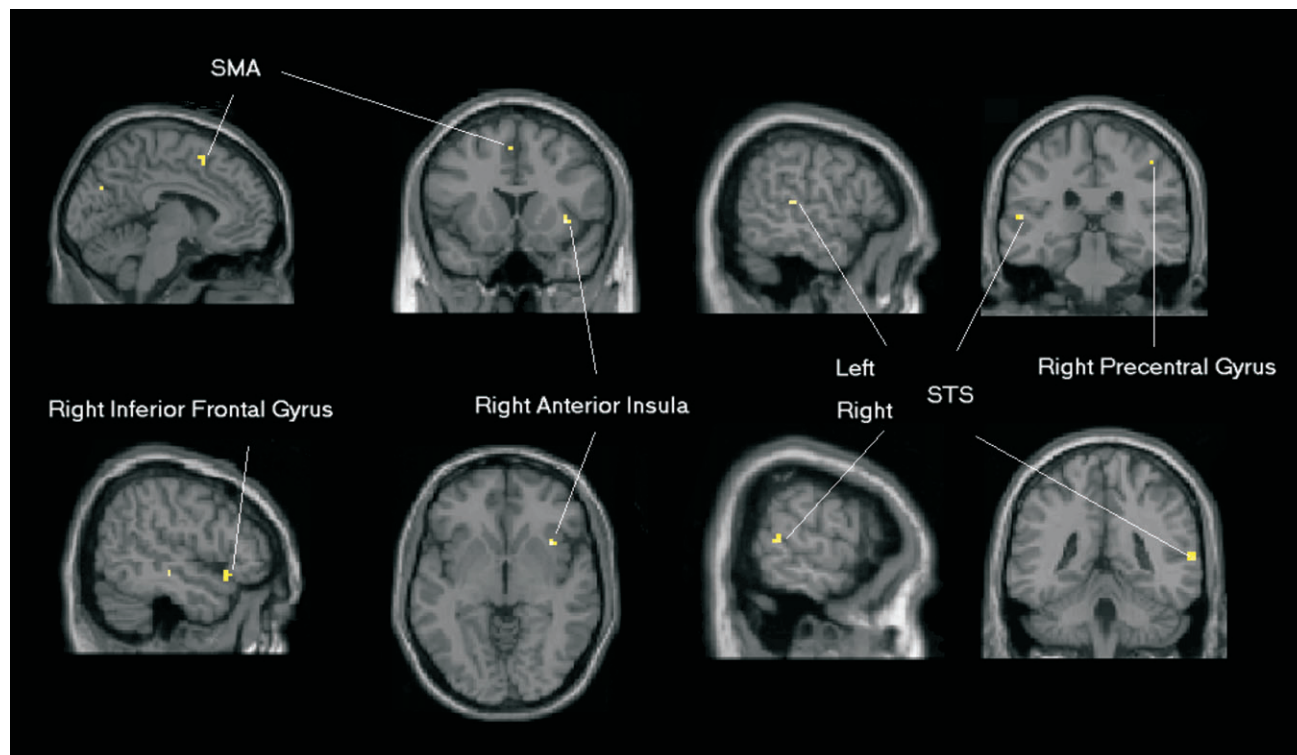

Figure 3. Brain regions showing significant activities for EEI. For coronal and axial sections, right is right and left is left.

Table 2

Sites where neural activation was associated with interference effect of emotion expression (for overall interference, $P < 0.001$, uncorrected; for highest 20% and lowest 20% interference, $P < 0.05$, with small volume correction of 10 mm radius)

BA	Overall interference				Highest 20% interference				Lowest 20% interference			
	Stereotaxic coordinates			Z-score	Stereotaxic coordinates			Z-score	Stereotaxic coordinates			Z-score
Right precentral gyrus (4)	45	−24	48	3.82	39	−29	51	2.26	53	−12	48	2.48
Right IFG (47)	50	17	−11	3.25	50	26	4	2.15	50	20	−11	2.30
SMA (6)	−3	9	55	3.60	−3	17	52	2.72				
Left STS (22)	−53	−29	10	3.56	−65	−43	15	2.65				
Right STS (22)	65	−40	8	3.49	62	−46	8	3.28	53	−60	22	3.12
Right middle temporal gyrus (21)	50	−24	−9	3.66	62	−35	−1	3.21	56	−43	2	2.42
Left lingual gyrus (18)	−21	−76	−11	3.93	−24	−79	−14	3.67	−30	−88	−5	3.50
Cuneus (7)	−9	−71	31	3.84	6	−68	42	3.85	6	−68	31	2.64
Right anterior insula	36	12	−1	3.74	36	29	−4	3.15	50	9	−3	2.05
Thalamus	6	−32	4	3.66	12	−29	1	3.32	8	−20	4	2.47
Right cerebellum (semilunar lobule)	24	−75	−37	3.73	27	−75	−34	2.22	28	−60	−27	2.97

Note: After taking the SPM of Simon task ($P = 0.01$, uncorrected) as an exclusive mask, the result is exactly the same.
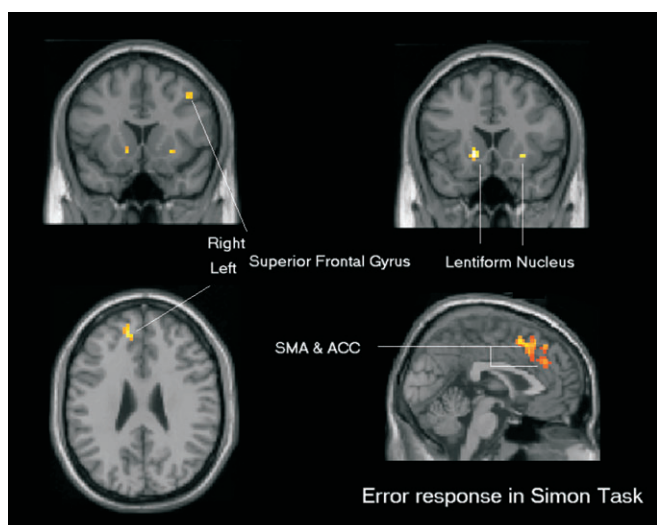

Figure 4. Brain regions showing significant activities for the interference of Simon task. For coronal and axial sections, right is right and left is left. The brain activities related to error response of Simon task is illustrated at the right lower corner.

Table 3

Sites where neural activation was associated with interference effect of Simon task (uncorrected, $P < 0.001$)

BA	Stereotaxic coordinates			Z-score
Left superior frontal gyrus (9)	−12	48	22	3.81
Right superior frontal gyrus (9)	42	16	38	3.46
Right superior temporal gyrus (22)	50	−6	−2	3.27
Right parahippocampal gyrus (36)	30	−35	−8	3.75
Right fusiform gyrus (37)	45	−53	−20	3.50
Left precuneus (7)	−9	−71	42	4.21
Left insula	−45	0	−3	4.10
Left lentiform nucleus	−15	17	−6	4.42
Right lentiform nucleus	27	17	−6	3.73
Left cerebellum (semilunar lobule)	−33	−72	−39	3.58

Table 4

Correlation map constructed from intensity rating and brain responses (discordant > concordant; uncorrected, $P < 0.001$)

BA	Stereotaxic coordinates			Z-score
Left IFG (9)	−53	13	24	3.26
Left IFG (47)	−42	26	−4	3.58
Right IFG (47)	48	23	−11	3.45
Left middle frontal gyrus (9)	−30	25	37	3.55
Right middle frontal gyrus (9)	45	25	26	3.35
Right middle frontal gyrus (6)	42	14	55	3.36
Right medial frontal gyrus (6)	9	−23	56	4.11
Right orbitofrontal gyrus (11)	27	43	−15	3.40
Left STS (22)	−53	−38	7	3.55
Left middle temporal gyrus (37)	−48	−44	−3	3.69
Right anterior insula	39	17	−11	4.01
Left cerebellum (tuber)	−33	−83	−29	3.42
Left cerebellum (uvula)	−3	−65	−27	3.73

Table 5

The rating results of ERQ and EQ and the correlation coefficients with activity at 4 regions of interest

	ERQ-supp	EQ-er	Mean score of rating			
Right IFG	0.62*	−0.39	ERQ-reap	31.64	EQ-ce	12.50
Right anterior insula	0.29	0.23	ERQ-supp	13.71	EQ-er	11.21
Left STS	0.30	−0.68**	ERQ-all	45.36	EQ-ss	6.86
Right STS	−0.26	0.09			EQ-all	38.36

Note: reap: reappraisal, supp: suppression, ce: cognitive empathy, er: emotion reactivity, ss: social skills, all: total score.
*$P = 0.017$, **$P = 0.008$.

At a psychological level, the EEI effect may reflect the greater motoric effort required to overcome a prepotent imitative facial expression in order to express a discordant emotion. Correspondingly, the brain regions observed in association with EEI include right IFG (BA 47), precentral gyrus, and medial prefrontal cortex (BA 6). The latter location (for facial movement) reinforces the notion of somatotopy within SMA (Chainay et al. 2004). The "pars opercularis" within right IFG, BA 44, is implicated in imitation network and regarded as part of a mirror neuron system (Carr et al. 2003; Rizzolatti and Craighero 2004; Lee et al. 2006). Mirror neurons, cells sensitive to both observed and self-initiated actions, provide a putative neural substrate for imitative behavior and simulatory representations of others. EEI may reflect the engagement of this mirror neuron system wherein the expression of discordant facial emotion overrides a prepotent automatic mimicry or mirror neuron response. In an earlier study, we demonstrated enhanced activity within right BA 44 during emotional facial mimicry that reflected parametrically the degree of facial musculature movement (Lee et al. 2006). Interestingly, in the present study, EEI-related

activity within right IFG extended into the neighboring, BA 47 and demonstrated a parametric relationship with intensity of conflicting emotion. One interpretation, arising from our previous study and those of others (Hariri et al. 2000; Eisenberger et al. 2003; Lee et al. 2006), is a modulatory role of BA 47 in suppressing implicit/automatic mimicry or mirror responses generated within BA 44.

One strategy, that subjects may have drawn upon to overcome interference during perception of a discordant emotional expression, is the engagement and amplification of representations of the intended expression. Within our imaging data, the activity of one brain region, right anterior insula, putatively reflected this compensatory representational enhancement. Right anterior insula is implicated in second-order representations of emotional state, including feelings arising from the interpretation of interoceptive responses and self-generated emotion (Reiman et al. 1997; Critchley et al. 2004). In the present study, right anterior insula activation was observed during EEI (both categorically and parametrically), reflecting at least the emotional effort required for discordant expressive responses. This account is concordant with the general notion that the insula is preferentially involved in the evaluative, experiential, or expressive aspects of internally generated emotions (Reiman et al. 1997; Phan et al. 2002).

We had not predicted a priori that STS activity would be engaged during the expression conflict task. STS is implicated in sensory processing of changeable aspects of face stimuli, including facial expressions (Puce et al. 1998; Winston et al. 2004) and corresponding representations of social signals (rather than motoric expression). Nevertheless, in our previous study (in which subjects mimicked facial expressions), we observed a parametric relationship between STS activity and magnitude of imitative facial movement (Lee et al. 2006). Together, these 2 studies demonstrate a role for STS that surpasses passive processing and representation of social signals. Rather STS cortical activity is context sensitive, in that it is modulated as a function of the facial expression held by the subject. In EEI, increased STS activity may facilitate processing and appraisal of social reactions evoked by the volitional expression of a discordant emotion.

S–R conflict and interference were not associated with enhanced dACC activity in either the emotion expression task or the Simon task. In cognitive tasks, dACC activity is implicated in control processes that include attentional demand, executive control, error detection, response monitoring, response inhibition, set shifting, attentional selection, strategy formation, and autonomic control (Paus et al. 1998; Carter et al. 1999; Bush et al. 2000; Gehring and Fencsik 2001; Critchley et al. 2003, 2005). Interference effects do not always evoke activity enhancement in dACC/preSMA. Thus during a Simon interference task, Maclin et al. (2001) proposed that anterior cingulate cortex (ACC) is particularly engaged where there is a conflict across modalities whereas within modality conflict is processed in regions dedicated to that specific functional modality. Besides, it has been reported that ACC does not show differential responding when events occurred with equal frequency, as in our design (Braver et al. 2001). Our own observation during the Simon task may endorse these views, observing frontostriatal activity changes consistent with previous reports (Rubia et al. 2006).

Our imaging findings of EEI may reflect 3 component mechanisms: enhanced motoric effort, subjective (actively generated) feeling state, and enhanced social signal processing. Correspondingly, we examined the relationship between activity in right IFG (BA 47), right anterior insula, and bilateral STS and interindividual differences in behavioral and subjective emotional style. Our observation that positive correlations between BA 47 activity and the suppression subscore of ERQ supports an account in which BA 47 modulates (or inhibits) automatic emotional expressions, perhaps via connectivity between BA 44 and premotor region. Thus, individual differences in the ability to suppress emotional responses are reflected in BA 47 activity during EEI. We also observed that activity in STS correlated negatively with individual scores of emotion reactivity (EQ-er reflects the tendency to react emotionally to the emotions of others; Lawrence et al. 2004). In the light of our extended integrative account of STS function, we suggest that a tendency toward enhanced emotional reactivity may enhance efficiency with which STS responses integrate the representation of perceived social signals with internal behavioral goals.

The EEI and Simon tasks represent different tasks, notably in type of stimuli, in mode of response and relative differences in the timing of cue and target. Each elicits a specific interference effect (emotion-response and cognition-response dimension, respectively). There are therefore a number of contributing factors that may account for differences between the tasks in the neural substrates for interference. First, the processing of the stimuli themselves may confound activity relating to conflict, evoking distinctive patterns of brain activation, which was related to face–object and spatial sensory representations instead of to the interference effect per se. Nevertheless, we attempted to address this by matching closely perceptual and response level requirements within the 2 tasks. Thus, after subtraction of discordant and concordant conditions, the neural centers mediating interference effects should be identified independently of presented stimuli and response demands. Further, if higher cognitive function (including different attention load) differentially modulated processing of S–R mismatch, we would anticipate differential brain responses within fusiform face area and superior parietal regions. The absence of significant effects at these loci supports the validity of our contrasts. Second, in our design, discordant and concordant conditions were balanced in terms of trial number (i.e., equal frequency), which minimized performance error and eliminated the possible confound of "frequency effect" in our interference brain map. As a consequence, the brain map of EEI did not interact with any cognitive effort required to overcome habitual responses inherent in design. Other studies have focused on this experimental manipulation of response competition (Braver et al. 2001). Third, although task difficulty may contribute to relative differences in interference-related brain activity, particularly within IFG (BA 47; Paus et al. 1998; Gould et al. 2003; Stricker et al. 2006), it is unlikely to account for the differences that we observed between EEI and Simon task activity. Behaviorally, both tasks produced correct response rates higher than 95% and 90% before and during experiments, indicating similar difficulty level. Further, correlation between the activity at BA 47 and STS with personal emotion regulation and empathy score underlines their roles in emotional expression control. Nevertheless, although we were unable to identify a common center for processing interference of EEI and Simon, this null finding does not exclude the recruitment of common centers for processing response conflict at higher levels of task demand and difficulty. Interestingly, a recent fMRI paper of emotion

go/nogo, where cognitive go/nogo served as a nonemotional comparison, also revealed distinct activation patterns (Shafritz et al. 2006). This observation complements our own evidence to imply that emotion-response inhibition and interference recruit additional or distinct neural substrates to cognitive control tasks and argue that there is no generic neural circuitry mediating all types of behavioral interference.

In summary, our study demonstrated a novel interference effect at the level of expressed emotion with important implications for adaptive social and motivational behavior. Using neuroimaging, we delineated centers of regional brain activity engaged during EEI and distinguished this activity pattern from activity engendered by nonemotional interference in a Simon task. EEI enhanced activity across distributed neural substrates including anterior right IFG (BA 47), SMA (facial area), posterior STS, and right anterior insula, reflecting motoric, perceptual, and experiential modules of emotional processing. BA 47 and STS activity during EEI further predicted individual differences in personality measures of regulatory emotional control and reactive emotion empathy. Our study highlights the neural specificity underlying EEI.

Notes

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