Emotion Perception and Executive Control Interact in the Salience Network During Emotionally Charged Working Memory Processing

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Abstract: Processing of emotional stimuli can either hinder or facilitate ongoing working memory (WM); however, the neural basis of these effects remains largely unknown. Here we examined the neural mechanisms of these paradoxical effects by implementing a novel emotional WM task in an fMRI study. Twenty-five young healthy participants performed an N-back task with fearful and neutral faces as stimuli. Participants made more errors when performing 0-back task with fearful versus neutral faces, whereas they made fewer errors when performing 2-back task with fearful versus neutral faces. These emotional impairment and enhancement on behavioral performance paralleled significant interactions in distributed regions in the salience network including anterior insula (AI) and dorsal cingulate cortex (dACC), as well as in emotion perception network including amygdala and temporal-occipital association cortex (TOC). The dorsal AI (dAI) and dACC were more activated when comparing fearful with neutral faces in 0-back task. Contrarily, dAI showed reduced activation, while TOC and amygdala showed stronger responses to fearful as compared to neutral faces in the 2-back task. These findings provide direct neural evidence to the emerging dual competition model suggesting that the salience network plays a critical role in mediating interaction between emotion perception and executive control when facing ever-changing behavioral demands. *Hum Brain Mapp 35:5606–5616, 2014.* © 2014 Wiley Periodicals, Inc.

INTRODUCTION

The ability to resolve emotional interference and maintain goal-directed behavior is a cardinal feature of rapid behavioral adaption in face of changing environmental demands [Barrett et al., 2004; Pourtois et al., 2013]. A wealth of behavioral research has documented that processing of emotion-laden stimuli can either hinder or facilitate ongoing cognitive processing depending on task demands at hand [Stokes et al., 2013], thereby leading to either emotional impairment [Dolcos and McCarthy, 2006; Gray et al., 2002; Habel et al., 2007; Mitchell and Phillips, 2007] or enhancement [Erk et al., 2007; Grimm et al., 2012; Lindström and Bohlin, 2011] of higher order cognitive functions such as working memory (WM). Although these paradoxical effects have been demonstrated in many behavioral studies, little is known about the neural mechanisms underlying interactions between emotion and cognition.

Psychological accounts posit that interactions between emotion and cognition result from the competition between emotional and cognitive processes for limited information processing capacity [Desimone and Duncan, 1995; Lavie et al., 2004; Park et al., 2007; Pessoa, 2009]. Early attention models, for instance, suggest that effects of emotion on cognitive processing may be related to competitive interactions between stimulus-driven bottom-up processing and top-down selective attention toward goal-relevant information while resolving goal-irrelevant interference [Desimone and Duncan, 1995; Lavie et al., 2004]. More recent dual competition models further suggest that emotional and cognitive processes, when simultaneously operated, compete for limited resources at both lower perceptual and higher executive control levels. Moreover, whether emotion can be beneficial or harmful for ongoing cognitive processing appears to depend on task demands (e.g., WM-load). Specifically, processing of emotional stimuli may disturb ongoing cognitive processing under conditions with low task-demand, because strong emotional arousal and/or valance draw attention away from task at hand [Pessoa, 2009]. On the other hand, processing of emotional stimuli may enhance cognitive performance under high task-demanding conditions, because the priority of executive control appears to over-ride emotional interference [Lindström and Bohlin, 2011]. For example, fearful compared to neutral faces can impair target detection under low perceptual load conditions [Bishop et al., 2004, 2007], whereas participants in WM tasks with emotional words [Grimm et al., 2012] and angry faces [Jackson et al., 2009; Langeslag et al., 2009] as stimuli exhibit better performance in a high task-demanding condition. These interactive effects between emotion and higher order cognitive functions have been thought to result from interplay of the brain systems underlying executive control and emotion perception [Gray, 2004; Gray et al., 2002; Pessoa, 2009]. Direct evidence at a neural level, however, is lacking in support of this account for emotion–cognition interactions.

There is now emerging evidence from human brain imaging studies suggesting that the AI and dorsal ACC (dACC), core regions of the salience network [Seeley et al., 2007], play a critical role in mediating interplay of multiple brain systems involved in emotion perception and executive control [Menon, 2011; Menon and Uddin, 2010; Pessoa, 2009]. Anatomically, core salience network regions such as the AI and dACC maintain strong reciprocal connections with an emotional perception network comprising the amygdala and ventral sensory pathways [Krämer et al., 2014]. This emotional perception network is suggested to be critical for perceptual processing of emotional stimuli [Butti and Hof, 2010; Hermans et al., 2011; Sabatinelli et al., 2011] and the fronto-parietal network are deemed important for higher level executive control [Bush et al., 2000; Eckert et al., 2009; Uddin and Menon, 2009]. Converging evidence from meta-analysis of task-related neuroimaging studies [Pessoa, 2009] as well as resting-state functional connectivity [Cauda et al., 2011], for instance, have shown that the salience network is not only involved in emotion perception but also engaged in executive control such as WM [Menon and Uddin, 2010]. Thus, the salience network is thought to be an integrative hub of bridging communication between emotion perception and executive control networks [Craig, 2009; Kurth et al., 2010]. On the one hand, the higher salience network activity under low WM condition might impair performance because emotion processing takes up resources that would be otherwise available for executive control [Bishop, 2009; Pessoa, 2009]. On the other hand, enhanced salience network activity might help in keeping attention under low task-demanding conditions because the salience network is also involved in focal attention [Eckert et al., 2009; Menon and Uddin, 2010; Nelson et al., 2010]. Under task-demanding conditions, however, higher activities of salience and emotion perception networks might override activity in the executive control network leading to impaired performance when WM-load is high [Perlstein et al., 2002]. In addition to the salience and executive networks involved in emotional WM processing [Levens and Phelps, 2010], other regions in emotion perception network might be recruited to facilitate WM processing when

emotional stimuli are used in the task [Jackson et al., 2008], thus improve WM performance. Hence, it remains largely elusive how the salience network, coordinating with perceptual and executive networks, enables these paradoxical effects of emotion on WM processing.

Here we conducted a functional magnetic resonance imaging (fMRI) study by implementing an emotional WM paradigm to investigate how processing of emotional stimuli can facilitate and hinder ongoing WM processing. In this paradigm, the emotional content of stimuli and the WM-load are manipulated within a full factorial design. Participants performed an emotional N-back task with sequentially presented face stimuli that had either a fearful or neutral expression, in which they were asked to identify whether the identity of the current face is identical with the one presented two trials before (i.e., 2-back, higher WM-load) or with a certain target face presented before each block (i.e., 0-back, lower WM-load). According to the dual competition model and previous studies on emotion-cognition interactions, we expect that emotional faces, relative to neutral faces, would improve WM performance in a high WM-load condition, while impair task performance in a low WM-load condition. Furthermore, these behavioral effects would be associated with interactions between emotion and WM-load in the salience network and particularly in the AI and dACC.

MATERIALS AND METHODS

Participants

Twenty-five young, healthy, right-handed college students with normal or corrected-to-normal vision participated in this study. Participants' mean age was 23.14 ± 1.83 years, ranged from 20 to 28. All participants reported no history of neurological or psychiatric disorders. Given that for this study we were not interested in sex differences, we restricted our study to male participants to rule out that potential gender differences as reported by [Koch et al., 2007; Schoofs et al., 2013] would affect our results. Written informed consent was obtained before the experiment in accordance with local ethical board requirements. Data from three participants were excluded from further analyses due to excessive head movement (larger than 3 mm or 3°) during fMRI scanning.

Cognitive Task and Procedures

A blocked-design emotional N-back task was adapted from the paradigm used in [Qin et al., 2009], with a 2-by-2 within-subject factorial design including an emotion factor (fearful vs. neutral faces) and a WM-load factor (0-back vs. 2-back). Specifically, there were four experimental conditions, including (1) a 0-back task with neutral faces as stimuli (0N), (2) a 2-back task with neutral faces (2N), (3) 0-back with fearful faces (0F), and (4) 2-back with fearful

faces (2F). Each condition was cycled six times in a pseudo-random manner with 0N and 2N or 0F and 2F not successively presented. A total of 20 faces with unique identity (10 neutral and 10 fearful; 50% males) were selected from a standardized Chinese Affective Database [Gong et al., 2011]. Each block consisted of a sequence of 15 faces. As shown in Figure 1, each block started with a cue presentation with 2.18 s duration followed by faces presented for 0.5 s one by one interleaved with a blank screen of 1 s. Each block lasted 24.5 s. Blocks were interleaved with fixation baseline with jittered duration of 4 to 8 s (average 6 s). There were three, four, or five targets in each block, which was counterbalanced across different blocks and participants.

In the 0-back condition, participants were asked to judge whether the face identity of the current item matches with the target face presented prior to each block. In the 2-back condition, participants were asked to judge whether the face identity of the current item matches with the item that appeared two positions back in the sequence. Participants were instructed to make a button press with their right index finger when detecting a target. The N-back task lasted about 12.3 min. Prior to the fMRI experiment, participants were asked to practice the task with eight blocks outside the MR scanner (two blocks for each condition) to familiarize them with the task procedure. Stimuli from this practice session were not used in the formal experiment.

Functional MRI Data Acquisition

During fMRI scanning, whole brain $T2^*$-weighted echo planar imaging scans were acquired with a Siemens Trio 3.0 T MR-scanner using an ascending slice acquisition sequence with the following parameters: 37 axial slices, repetition time 2.18 s, echo time 25 ms, 80° flip angle, slice matrix size 64×64, slice thickness 3.0 mm, slice gap 0.3 mm, field of view (FoV) 212×212 mm^2. Three hundred eighty-six volumes were acquired in total. High-resolution structural images were acquired for registration purposes using a T1-weighted three-dimensional magnetization-prepared rapid gradient-echo (MP-RAGE) sequence: TR 1.9 s, TE 2.52 ms, flip-angle 9°, 192 contiguous sagittal slices, slice matrix size 256×256, FoV 256×256 mm^2, and resolution 1 mm isotrophic.

Data Analysis

Image preprocessing and statistical analysis was performed using SPM8 (http://www.fil.ion.ucl.ac.uk/spm). Functional images were rigid-body motion corrected and the mean image was coregistered to each participant's T1-weighted MR image. Then the coregistration parameters were used to register all aligned functional scans to the T1. Subsequently, images were transformed into a common stereotactic space by matching the T1 image onto the
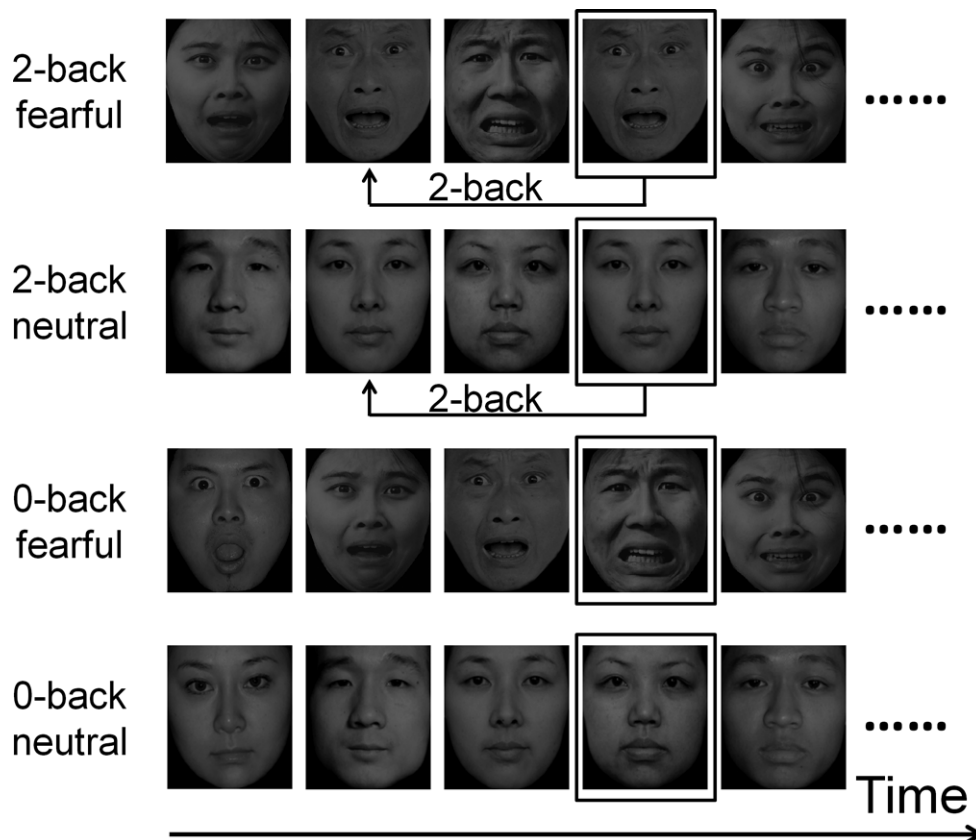
Figure 1.

Experimental design for emotional N-back WM task. Each block consists of a sequence of 15 faces. In the 0-back condition, participants were asked to detect whether the identity of current face on the screen was same as the identity of a fixed face presented right before each block. In the 2-back condition, partici- pants were asked to detect whether the identity and emotional expression of current face had appeared two items back in the sequence. Notes: Targets are marked by the black square frame for displaying purposes.

MNI152 T1-template, and resampled into 2 mm isotropic voxels. Finally, images were spatially smoothed by convolving with an isotropic 3D Gaussian kernel (8 mm full width at half maximum). The data were statistically analyzed using general linear models and statistical parametric mapping.

To assess neural activity associated with neutral and fearful face presentation while performing the N-back WM tasks, the four conditions (0N, 2N, 0F, and 2F) were modeled separately as boxcar regressors and convolved with the canonical hemodynamic response function in SPM8. Additionally, six realignment parameters were included to account for movement-related variability. The analysis, furthermore, included high-pass filtering using a cutoff of 1/128 Hz, global intensity normalization, and serial correlations correction using a first-order autoregressive model.

The contrast parameter images for all four conditions relative to the fixation baseline generated at the individual subject level were submitted to a second-level group analysis by treating participants as a random factor. A 2-by-2 full-factorial analysis of variance (ANOVA) was conducted with WM-load (0- versus 2-back) and emotion (neutral versus fearful) as within-subject factors. All reported activations were whole brain family-wise error (FWE) corrected at the voxel level.

Given our prior interest for the salience network including the AI and dACC, these regions were submitted to a small volume FWE correction procedure by taking from independent functional ROIs atlas of the anterior saliency network [Shirer et al., 2012]. Because of our particular interest to the amygdala, a bilateral amygdala anatomical mask, defining in the Wake Forest University Pickatlas [Maldjian et al., 2003, 2004], was been used for small volume correction analysis. To further visualize neural activation patterns for each of our four experimental conditions, parameter estimates were extracted from clusters showing
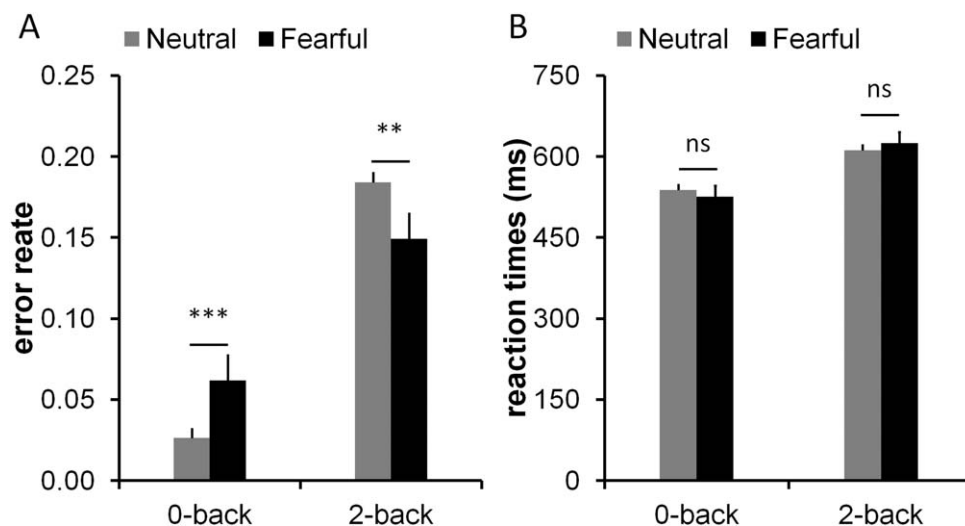
Figure 2.

Behavioral performance on emotional WM task. Histograms depict error rate (A) and reaction times (B) when performing 0-back and 2-back task with fearful and neutral faces. Notes: Error bars represent standard error of mean.

significant interaction effects between factors of emotion and WM-load from each subject using MarsBaR [Brett et al., 2002].

RESULTS

Behavioral Results

Two separate repeated-measure analyses of variance (ANOVAs) for reaction times (RTs) of correct responses and error rate were conducted with emotion and WM-load as within-subject factors. We found robust main effects of WM-load for RTs [$F (1, 21) = 21.08$, $P < 0.001$] and error rate [$F (1, 21) = 105.97$, $P < 0.001$] and a significant interaction between WM-load and emotion [$F (1, 21) = 21.69$, $P < 0.001$] for error rate. Further analyses revealed that participants responded faster and made less errors under low compared to high WM-load. Critically, participants showed higher error rates when performing the 0-back task with fearful compared to neutral faces (t (21) = 4.95, $P < 0.001$), conversely, participants made less errors when performing the 2-back task with fearful compared to neutral faces (t (21) = 3.01, $P = 0.007$; Fig. 2). These results indicate that WM processing is strongly modulated by emotion, with fearful faces impairing performance in the 0-back but enhancing performance in the 2-back task.

Neuroimaging Results

Main effect of WM-load and emotion

By contrasting 2-back with 0-back conditions while collapsing across fearful and neutral conditions, we replicated

robust activations of a frontal parietal WM-related network including the bilateral DLPFC (local maxima at [40 32 34] and [−44 26 32], $P < 0.05$, family-wise error (FWE) corrected), bilateral intraparietal cortex (local maxima at [42 −48 46] and [−36 −54 46], $P < 0.05$, FWE corrected, Fig. 3a), and other related regions listed in Table I. The opposite contrast yielded significant activation in the bilateral medial temporal lobe extending into the amygdala (local maxima at [26 −8 −20] and [−24 −8 −20], $P < 0.05$, FWE corrected) and in regions of the default mode network including the posterior cingulate cortex (local maxima at [−6 −26 48] and [−6 −52 32], $P < 0.05$, FWE corrected) and the medial prefrontal cortex (MPFC) extending into the orbitofrontal cortex (local maxima at [−10 58 30] and [−8 60 12], $P < 0.05$, FWE corrected; see Table I and Fig. 3b).

By contrasting the fearful with neutral conditions irrespective of WM-load, we found significant clusters at the fusiform gyrus (local maxima at [−42 −46 −26], $P < 0.05$, FWE corrected), inferior occipital gyrus (local maxima at [30 −78 −14], $P < 0.05$, FWE corrected), and superior/middle temporal gyrus (local maxima at [−54 −54 8] and [54 −60 2], $P < 0.05$, FWE corrected, Fig. 3c). Contrasting neutral with fearful faces did not return any significant results. This pattern of results is highly consistent with findings from previous studies in variety of cognitive tasks with emotional faces as stimuli [Sabatinelli et al., 2011; Vuilleumier and Pourtois, 2007].

Interaction between WM and emotion

To identify the neural correlates of the emotional impairment effect under low WM-load, we conducted a
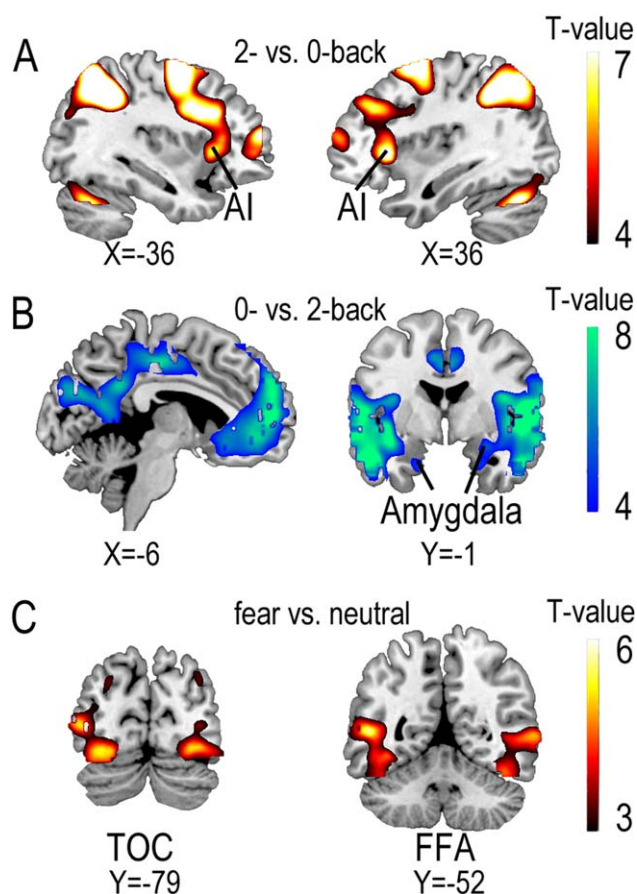
Figure 3.

Brain regions showing significant main effects of WM-load and emotion. (A) Representative views of significant clusters of activation in the fronto-parietal network (shown in hot color) and deactivation in the default mode network (showed in winter blue). (B) Representative views of significant clusters in the amygdala. (C) Representative views of significant clusters in the posterior visual cortex and fusiform face area (FFA) and temporal-occipital association cortex (TOC) derived from the contrast between fearful faces versus neutral condition. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

contrast of fearful with neutral conditions for the 0-back versus 2-back task. As shown in Table II, we found significant clusters in the bilateral dorsal AI (dAI, local maxima at [36 20 −8], $P < 0.05$, FWE corrected, and [−34 14 −6], $P < 0.05$, SVC) and a strong trend for the dACC (local maxima at [8 30 38], $P = 0.05$, SVC). Follow-up simple effect analyses revealed increased activation in the dAI ($P < 0.05$, SVC; Fig. 4) and dACC ($P < 0.05$, SVC, Fig. 4) when performing the 0-back task with fearful compared to neutral faces as stimuli. In contrast, we observed reduced activation in the dAI ($P < 0.05$, SVC; Fig. 4A) when performing the 2-back task with fearful compared to neutral faces as stimuli.

Given that the salience network activity has been shown related to error processing [Carter et al., 1998; Ham et al., 2013], we conducted an additional control analysis by including error rate as a covariate variable of no interest. This analysis again revealed a very similar pattern of interaction effect between emotion and WM in the right dAI ($P < 0.05$, SVC) as well as dACC ($P < 0.005$, uncorrected).

To identify the neural correlates of emotional enhancement effect under high WM-load, we conducted a contrast of fear with neutral conditions in the 2-back versus 0-back task. We found significant clusters in the superior occipital gyrus (local maxima at [46 −80 26], $P < 0.05$, FWE corrected), middle occipital gyrus (local maxima at [32 −96 18], $P < 0.05$, FWE corrected), and middle temporal gyrus (local maxima at [32 −68 14], $P < 0.05$, FWE corrected, Fig. 4C). We observed significant interaction in the left amygdala (local maxima at [−16 −4 −26], $P < 0.05$, SVC). Simple effect analyses revealed increased activation in the left amygdala and temporal-occipital association regions when performing the 2-back task with fearful compared to neutral faces.

DISCUSSION

In this study, we examined whether differential processing in salience and the emotion perception network could explain competition between emotion perception and executive control involved in emotional WM processing. Behaviorally, participants showed poorer performance in the 0-back task with fearful than neutral faces as stimuli, whereas participants performed better in the 2-back task with fearful compared to neutral faces. Critically, we found interactions between emotion and WM-load in the salience and emotion perception networks. That is, the emotional impairment observed in the 0-back task is accompanied with higher activation in the salience network including dAI and dACC, whereas emotional improvement in the 2-back task is accompanied with relatively reduced activation in the right dAI within the salience network as well as higher activation in the amygdala and middle occipital gyrus within the emotion perception network. These results provide neural evidence for the dual competition model [Pessoa, 2009], which suggests a mediating role of the salience network in the interaction between an emotion perception network and an executive control network.

Behaviorally, we observed an emotional impairment under low WM-load condition, whereas enhancement effects on WM performance under high WM-load condition. These effects are in line with findings from previous studies that angry faces can interfere with gender judgment when concurrent WM demands are low [Van Dillen and Koole, 2009], whereas negative affect [Gray et al., 2002], emotionally arousing stimuli [Grimm et al., 2012; Jackson et al., 2008; Langeslag et al., 2009; Lindström and Bohlin, 2011], and mild psychological stress [Cousijn et al.,

TABLE I. Brain regions showing main effect of working memory load, emotion

Brain regions	Cluster size	T value	Local maximum MNI 152 coordinates		
			x	y	z
2-back > 0-back					
Superior/Inferior parietal lobule	1794	12.48[a]	−36	−54	46
		10.96[a]	−10	−74	52
		10.50[a]	42	−48	46
Superior/Middle/Inferior frontal gyrus	4330	11.56[a]	−44	26	32
		11.27[a]	−32	−2	52
		10.60[a]	−4	16	52
Anterior Insula	265	7.88[a]	−34	54	14
		5.62[a]	−38	48	4
Fusiform gyrus/Lingual gyrus	125	7.98[a]	30	−62	−32
		6.57[a]	10	−78	−26
		6.25[a]	22	−80	−20
Cerebellum Posterior Lobe	220	7.00[a]	−34	−62	−32
0-back > 2-back					
Medial frontal gyrus	4456	9.00[a]	−10	58	30
		8.84[a]	−8	60	12
		8.10[a]	−8	46	−6
Superior temporal gyrus	3805	8.79[a]	58	−2	8
		8.77[a]	50	−28	22
		8.03[a]	52	6	−28
Superior temporal gyrus	4438	8.79[a]	−52	0	−28
		7.68[a]	−56	−36	18
		7.08[a]	−42	−6	0
Hippocampus/Parahippocampa gyrus	411	8.51[a]	−30	−26	−14
Posterior cingulate gyrus	4144	7.87[a]	−6	−26	48
		7.66[a]	−6	−52	32
		7.47[a]	−8	−62	16
Middle temporal gyrus/Angular	204	7.53[a]	−54	−70	30
Hippocampus/Parahippocampa gyrus	296	7.10[a]	32	−12	−20
		5.75[a]	34	−32	−10
Postcentral gyrus	372	6.61[a]	20	−40	72
		5.76[a]	22	−48	66
Postcentral gyrus	346	6.36[a]	−28	−46	64
		5.75[a]	−20	−32	78
Amygdala	188	5.41[c]	26	−8	−20
		4.04[c]	32	2	−18
	133	4.33[c]	−24	−8	−20
		4.20[c]	−28	−6	−22
Fearful > neutral					
Fusiform gyrus	35	5.60[b]	−42	−46	−26
Inferior occipital gyrus	115	5.50[b]	30	−78	−14
	58	5.47[b]	−34	−82	−10
Middle occipital gyrus	80	5.66[b]	−46	−78	4
Superior/middle temporal gyrus	186	5.95[b]	−54	−54	8
	80	5.58[b]	54	−60	2

MNI, Montreal Neurological Institute in SPM8.
[a]Cluster-wise significance at a height threshold of $P < 0.001$ uncorrected and an extent threshold of 52 voxels; $P < 0.05$ whole-brain family wise error-corrected for multiple comparisons.
[b]Cluster-wise significance at a height threshold of $P < 0.005$ uncorrected and an extent threshold of 71 voxels, $P < 0.05$ small volume correction (SVC) for multiple comparisons.
[c]voxel-wise $P < 0.005$ uncorrected, small volume correction (SVC) procedure.

TABLE II. Brain regions showing interaction between WM-load and emotion

Brain regions	Cluster size	T value	Local maximum MNI 152 coordinates		
			x	y	z
[(0-back fear > 0-back neutral) > (2-back fear > 2-back neutral)]					
Dorsal anterior cingulate cortex	97	3.40[a]	8	30	38
		3.38[a]	8	36	22
Anterior insula	44	4.83[a]	36	18	−8
	4	3.31[a]	−34	14	−6
[(2-back fear > 2-back neutral) > (0-back fear > 0-back neutral)]					
Amygdala	5	3.97[a]	−16	−4	−26
Superior occipital gyrus	1273	4.10[b]	46	−80	26
Middle temporal gyrus		4.05[b]	32	−68	14
Middle occipital gyrus		3.78[b]	32	−96	18

MNI, Montreal Neurological Institute in SPM8; WM, working memory.
[a]voxel-wise $P < 0.005$ uncorrected, small volume correction (SVC) procedure.
[b]Cluster-wise significance at a height threshold of $P = 0.005$ uncorrected and an extent threshold of 1273 voxels, $P = 0.005$ small volume correction (SVC) for multiple comparisons.

2012] can enhance WM performance under high task-demanding conditions. This emotional impairment effect can be readily explained by the emerging dual competition model (Pessoa, 2009), positing that emotional and cognitive processes, when operating simultaneously, compete with each other for limited neural resources. Specifically, processing of emotional stimuli may interfere with ongoing cognitive processes [Van Dillen and Koole, 2009] when cognitive resources are not entirely devoted to goal-directed processing under a lower task demanding condition, such as during the 0-back task in our study. When more resources are required to achieve goal-directed behavior such as in the 2-back WM task here, however, the enhancement effect may be also related to enhance encoding of the identity of fearful faces than neural faces due to higher arousal for these faces. This is somewhat similar to findings from numerous studies suggesting higher engagement of amygdala and related perceptual regions in facial recognition and declarative memory for emotional than neural faces [Gothard et al., 2007] as well as other emotional stimuli [Kensinger et al., 2006, 2007]. Such classical emotion-induced boosting effects for emotionally stimuli in facial recognition and declarative memory [LaBar and Cabeza, 2006; Murty et al., 2010], however, cannot readily explain our observed emotional impairment under low WM-load. Future studies are required to dissociate differential effects of emotion on WM and declarative memory. It is worth to note that we focused on only fearful and neutral face processing in our design. Future studies are required to more thoroughly address how emotion arousal and valence modulate WM processing including positively valence stimuli. Together, our findings provide evidence to suggest that enhancement and impairment effects of emotional stimuli on WM processing appear to rely on the task demands at hand.

In parallel with the observed behavioral interactions, we found significant interactions between emotion and WM in the dAI and the dACC as well as the amygdala and middle occipital gyrus. The dAI and dACC, that is, the anatomical bridge between emotion perception network and executive control network, have been shown to be involved in not only emotion perception such as salience detection (e.g., Seeley et al. 2007) but also contribute to higher order executive processing (e.g., Menon and Uddin, 2010). In our study, the emotional content of stimuli are automatically capture participants' attention thereby induce an emotion processing which will compete with WM task at hand. In other words, performing an emotional WM task is analogous to a dual processing task involving both emotional and executive processes which are thought to rely on the salience network together with the emotion perception and fronto-parietal executive networks [Curtis and D'Esposito, 2003; Phelps et al., 2006].

More specifically, we observed higher salience network activity under low WM-load with fearful compared to neutral faces. This increased engagement of the salience network is in line with two separate studies reporting an increase in the salience processing under low perceptual load condition [Bishop et al., 2007; Lim et al., 2008]. It is conceivable that our observed increase activation in the salience network may be related to overwhelming emotional information flow into the salience network, thereby, interfering ongoing cognitive processing. The overwhelming emotional processing might due to tonically enhanced activity of emotion perception network (i.e., amygdala, medial temporal lobe) as well as reduced activity of executive control network under a lower task demanding circumstances [Clarke and Johnstone, 2013].

In contrast, under higher task-demanding conditions, increased allocation of cognitive resources for goal-directed behavior is typically associated with enhanced activation in salience network [Gu et al., 2013; Levens and Phelps, 2010], as we also observed for both neutral and fearful faces under the 2-back compared to 0-back. Due to
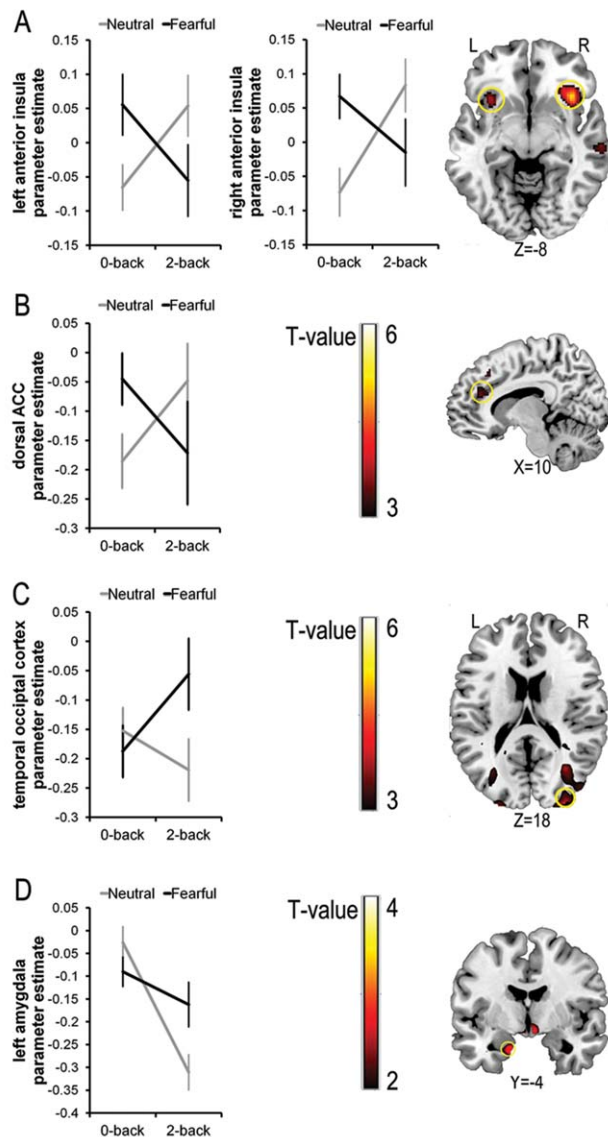
Figure 4.

Brain regions showing significant interactions between emotion and WM-load. (A) An axial view of significant clusters in the anterior insula (AI) and corresponding parameter estimates for four experimental conditions. (B) A sagittal view of significant cluster in the dorsal anterior cingulate cortex (dACC) and corresponding parameter estimates for four experimental conditions. (C) An axial view of significant cluster in the temporal-occipital association cortex (TOC) and corresponding parameter estimates for four experimental conditions. (D) A coronal view of significant cluster in the amygdala and corresponding estimates for four experimental conditions. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

more neural resources allocated to executive control network for achieving goal-directed behavior, less resources become available for the emotion perception network lead-

ing to less emotional interference [Bishop, 2009; Clarke and Johnstone, 2013; Lim et al., 2008]. Our observed relative reduction activation in the salience network in 2-back task with fearful faces was likely because the fearful faces benefit from additional perceptual processing and this reduces executive control requirement.

We found higher activation in the middle occipital gyrus and the left amygdala when performing 2-back task with fearful compared to neutral faces. These results are consistent with numerous studies reporting the posterior visual cortex and the amygdala are important for emotional face perception, suggesting strengthened neural representations for emotional stimuli [Kanske, 2012; Vuilleumier and Driver, 2007; Whalen, 1998]. This enhanced neural representation has been associated with an emotional enhancement effect on a variety of cognitive tasks, including perception, working memory as well as long-term memory [Ludmer et al., 2011; Scolari et al., 2008; Zhang and Luck, 2011]. It is well possible that our observed higher activation in the perceptual network may reflect an enhanced perceptual processing and better maintenance of fearful faces in high WM-load task [Langeslag et al., 2009], thus leading to facilitated top-down executive control processing, as evidenced by the emotional enhancement effect on 2-back WM performance.

In the present study, we observed the very prominent emotion-WM interaction effect in the dorsal portion of the insula. Based on recent neurocognitive models of the insula [Chang et al., 2013; Deen et al., 2011; Kelly et al., 2012; Uddin et al., 2014], the human insular cortex is a homogeneous structure encompassing multiple functional subdivisions which are thought to play an integrative role in emotion, cognition and interoception. Specifically, several recent studies suggested that there are three functional subdivisions of the human insular cortex, including a dorsal middle part of anterior insula functionally associated with higher cognitive task and executive control, a ventral part of anterior insula functionally related to emotion and autonomic function, a posterior part of insula related to pain, sensorimotor, as well as language-related topics [Chang et al., 2013; Nelson et al., 2010]. Furthermore, the most recent meta-analysis of human neuroimaging studies suggests that there are amount of coactivation across these three subdivisions as well as other brain network across a variety of cognitive, affective, and interocepative tasks [Uddin et al., 2014]. Critically, the dorsal anterior insula has been associated with salience detection, task switching and working memory, suggesting that dorsal anterior insula is the hub of information integration among cognitive, affective, and interocpetive domains [Chang et al., 2013; Deen et al., 2011; Kelly et al., 2012; Kurth et al., 2010; Uddin et al., 2014]. Therefore, we think that our observed effect in the dorsal portion of the anterior insula, together with the dorsal anterior cingulate cortex, most likely reflect an interplay of executive control and emotional perception in face of different task demands. This effect is in line with recent study reporting that the dorsal anterior insula

is an important hub for switching between the executive control network and the default mode network [Menon and Uddin, 2010; Sridharan et al., 2008; Uddin et al., 2014], as well as that the dorsal anterior insula influences our behavior by integrating interoceptive information from posterior insula and affective information from ventral anterior insula [Deen et al., 2011]. Our findings add evidence in support of this integrative role of the dorsal anterior insula in orchestrating access to emotion and cognitive systems.

In conclusion, our study demonstrates that processing emotional stimuli can either hinder or facilitate ongoing WM processing, depending on low or high levels of task demands. The dAI and dACC, core regions of the salience network, play a critical role in mediating the interaction between emotion perception and executive control involving in emotional WM processing. These findings provide important insights into our understanding of how the salience network mediates interactions between the emotion perception and executive networks to confer emotion–cognition interactions and rapid behavioral adaptation when facing ever-changing task demands.

REFERENCES

Barrett LF, Tugade MM, Engle RW (2004): Individual differences in working memory capacity and dual-process theories of the mind. Psychol Bull 130:553–573.

Bishop SJ (2009): Trait anxiety and impoverished prefrontal control of attention. Nat Neurosci 12:92–98.

Bishop SJ, Duncan J, Brett M, Lawrence AD (2004): Prefrontal cortical function and anxiety: controlling attention to threat-related stimuli. Nat Neurosci 7:184–188.

Bishop SJ, Jenkins R, Lawrence AD (2007): Neural processing of fearful faces: Effects of anxiety are gated by perceptual capacity limitations. Cereb Cortex 17:1595–1603.

Brett M, Anton J, Valabregue R, Poline J (2002): Region of interest analysis using an SPM toolbox. Presented at the 8th International Conferance on Functional Mapping of the Human Brain. Sendai, Japan. Vol. 16, pp 37–258.

Bush G, Luu P, Posner MI (2000): Cognitive and emotional influences in anterior cingulate cortex. Trends Cogn Sci 4:215–222.

Butti C, Hof P (2010): The insular cortex: a comparative perspective. Brain Struct Funct 214:477–493.

Carter CS, Braver TS, Barch DM, Botvinick MM, Noll D, Cohen JD (1998): Anterior Cingulate Cortex, Error Detection, and the Online Monitoring of Performance. Sci 280 747–749.

Cauda F, D'Agata F, Sacco K, Duca S, Geminiani G, Vercelli A (2011): Functional connectivity of the insula in the resting brain. Neuroimage 55:8–23.

Chang LJ, Yarkoni T, Khaw MW, Sanfey AG (2013): Decoding the role of the insula in human cognition: functional parcellation and large-scale reverse inference. Cereb Cortex 23:739–749.

Clarke R, Johnstone T (2013): Prefrontal inhibition of threat processing reduces working memory interference. Front Hum Neurosci 7:1–17.

Cousijn H, Rijpkema M, Qin S, van Wingen GA, Fernández G (2012): Phasic deactivation of the medial temporal lobe enables working memory processing under stress. Neuroimage 59: 1161–1167.

Craig AD (2009): How do you feel-now? The anterior insula and human awareness. Nat Rev Neurosci 10:59–70.

Curtis CE, D'Esposito M (2003): Persistent activity in the prefrontal cortex during working memory. Trends Cogn Sci 7:415–423.

Deen B, Pitskel NB, Pelphrey Ka (2011): Three systems of insular functional connectivity identified with cluster analysis. Cereb Cortex 21:1498–1506.

Desimone R, Duncan J (1995): Neural mechanisms of selective visual attention. Annu Rev Neurosci 18:193–222.

Van Dillen LF, Koole SL (2009): How automatic is "automatic vigilance"? The role of working memory in attentional interference of negative information. Cogn Emot 23:1106–1117.

Dolcos F, McCarthy G (2006): Brain systems mediating cognitive interference by emotional distraction. J Neurosci 26:2072–2079.

Eckert M a, Menon V, Walczak A, Ahlstrom J, Denslow S, Horwitz A, Dubno JR (2009): At the heart of the ventral attention system: The right anterior insula. Hum Brain Mapp 30: 2530–2541.

Erk S, Kleczar A, Walter H (2007): Valence-specific regulation effects in a working memory task with emotional context. Neuroimage 37:623–632.

Gong X, Huang Y, Wang Y, Luo Y (2011): Revision of the Chinese facial affective picture system. Chinese Ment Heal J 25:40–46.

Gothard KM, Battaglia FP, Erickson CA, Spitler KM, Amaral DG (2007): Neural responses to facial expression and face identity in the monkey amygdala. J Neurophysiol 97:1671–1683.

Gray JR, Braver TS, Raichle ME (2002): Integration of emotion and cognition in the lateral prefrontal cortex. Proc Natl Acad Sci USA 99:4115–20.

Gray JR (2004): Integration of emotion and cognitive control. Curr Dir Psychol Sci 13:46–48.

Grimm S, Weigand A, Kazzer P, Jacobs AM, Bajbouj M (2012): Neural mechanisms underlying the integration of emotion and working memory. Neuroimage 61:1188–1194.

Gu X, Liu X, Van Dam NT, Hof PR, Fan J (2013): Cognition-emotion integration in the anterior insular cortex. Cereb Cortex 23: 20–27.

Habel U, Koch K, Pauly K, Kellermann T, Reske M, Backes V, Seiferth NY, Stöcker T, Kircher T, Amunts K, Jon Shah N, Schneider F (2007): The influence of olfactory-induced negative emotion on verbal working memory: Individual differences in neurobehavioral findings. Brain Res 1152:158–170.

Ham T, Leff A, de Boissezon X, Joffe A, Sharp DJ (2013): Cognitive control and the salience network: An investigation of error processing and effective connectivity. J Neurosci 33:7091–7098.

Hermans EJ, van Marle HJF, Ossewaarde L, Henckens MJ a G, Qin S, van Kesteren MTR, Schoots VC, Cousijn H, Rijpkema M, Oostenveld R, Fernández G (2011): Stress-related noradrenergic activity prompts large-scale neural network reconfiguration. Science 334:1151–1153.

Jackson MC, Wolf C, Johnston SJ, Raymond JE, Linden DEJ (2008): Neural correlates of enhanced visual short-term memory for angry faces: An FMRI study. PLoS One 3:e3536.

Jackson MC, Wu C-Y, Linden DEJ, Raymond JE (2009): Enhanced visual short-term memory for angry faces. J Exp Psychol Hum Percept Perform 35:363–374.

Kanske P (2012): On the influence of emotion on conflict processing. Front Integr Neurosci 6:42.

Kelly C, Toro R, Di Martino A, Cox CL, Bellec P, Castellanos FX, Milham MP (2012): A convergent functional architecture of the

insula emerges across imaging modalities. Neuroimage 61: 1129–1142.

Kensinger E a, Garoff-Eaton RJ, Schacter DL (2007): How negative emotion enhances the visual specificity of a memory. J Cogn Neurosci 19:1872–1887.

Kensinger E a., Garoff-Eaton RJ, Schacter DL (2006): Memory for specific visual details can be enhanced by negative arousing content. J Mem Lang 54:99–112.

Koch K, Pauly K, Kellermann T, Seiferth NY, Reske M, Backes V, Stöcker T, Shah NJ, Amunts K, Kircher T, Schneider F, Habel U (2007): Gender differences in the cognitive control of emotion: An fMRI study. Neuropsychologia 45:2744–2754.

Krämer K, Bente G, Kuzmanovic B, Barisic I, Pfeiffer UJ, Georgescu AL, Vogeley K (2014): Neural correlates of emotion perception depending on culture and gaze direction. Cult Brain 2:21–57.

Kurth F, Zilles K, Fox PT, Laird AR, Eickhoff SB (2010): A link between the systems: functional differentiation and integration within the human insula revealed by meta-analysis. Brain Struct Funct 214:519–534.

LaBar KS, Cabeza R (2006): Cognitive neuroscience of emotional memory. Nat Rev 7:54–64.

Langeslag SJE, Morgan HM, Jackson MC, Linden DEJ, Van Strien JW (2009): Electrophysiological correlates of improved short-term memory for emotional faces. Neuropsychologia 47:887–896.

Lavie N, Hirst A, de Fockert JW, Viding E (2004): Load theory of selective attention and cognitive control. J Exp Psychol Gen 133:339–354.

Levens SM, Phelps EA (2010): Insula and orbital frontal cortex activity underlying emotion interference resolution in working memory. J Cogn Neurosci 22:2790–803.

Lim S-L, Padmala S, Pessoa L (2008): Affective learning modulates spatial competition during low-load attentional conditions. Neuropsychologia 46:1267–1278.

Lindström BR, Bohlin G (2011): Emotion processing facilitates working memory performance. Cogn Emot 25:1196–1204.

Ludmer R, Dudai Y, Rubin N (2011): Uncovering camouflage: Amygdala activation predicts long-term memory of induced perceptual insight. Neuron 69:1002–14.

Maldjian JA, Laurienti PJ, Burdette JH (2004): Precentral gyrus discrepancy in electronic versions of the Talairach atlas. Neuroimage 21:450–455.

Maldjian JA, Laurienti PJ, Kraft RA, Burdette JH (2003): An automated method for neuroanatomic and cytoarchitectonic atlas-based interrogation of fMRI data sets. Neuroimage 19:1233–1239.

Menon V (2011): Large-scale brain networks and psychopathology: A unifying triple network model. Trends Cogn Sci 15: 483–506.

Menon V, Uddin L (2010): Saliency, switching, attention and control: A network model of insula function. Brain Struct Funct 214:655–667.

Mitchell RLC, Phillips LH (2007): The psychological, neurochemical and functional neuroanatomical mediators of the effects of positive and negative mood on executive functions. Neuropsychologia 45:617–629.

Murty VP, Ritchey M, Adcock RA, LaBar KS (2010): fMRI studies of successful emotional memory encoding: A quantitative meta-analysis. Neuropsychologia 48:3459–3469.

Nelson SM, Dosenbach NUF, Cohen AL, Wheeler ME, Schlaggar BL, Petersen SE (2010): Role of the anterior insula in task-level control and focal attention. Brain Struct Funct 214:669–680.

Park S, Kim M-S, Chun MM (2007): Concurrent working memory load can facilitate selective attention: evidence for specialized load. J Exp Psychol Hum Percept Perform 33:1062–1075.

Perlstein WM, Elbert T, Stenger VA (2002): Dissociation in human prefrontal cortex of affective influences on working memory-related activity. Proc Natl Acad Sci USA 99:1736–1741.

Pessoa L (2009): How do emotion and motivation direct executive control? Trends Cogn Sci 13:160–166.

Phelps EA, Ling S, Carrasco M (2006): Emotion facilitates perception and potentiates the perceptual benefits of attention. Psychol Sci 17:292–299.

Pourtois G, Schettino A, Vuilleumier P (2013): Brain mechanisms for emotional influences on perception and attention: What is magic and what is not. Biol Psychol 92:492–512.

Qin S, Hermans EJ, van Marle HJF, Luo J, Fernandez G, Fernández G (2009): Acute psychological stress reduces working memory-related activity in the dorsolateral prefrontal cortex. Biol Psychiatry 66:25–32.

Sabatinelli D, Fortune EE, Li Q, Siddiqui A, Krafft C, Oliver WT, Beck S, Jeffries J (2011): Emotional perception: Meta-analyses of face and natural scene processing. Neuroimage 54:2524–2533.

Schoofs D, Pabst S, Brand M, Wolf OT (2013): Working memory is differentially affected by stress in men and women. Behav Brain Res 241:144–153.

Scolari M, Vogel EK, Awh E (2008): Perceptual expertise enhances the resolution but not the number of representations in working memory. Psychon Bull Rev 15:215–222.

Seeley WW, Menon V, Schatzberg AF, Keller J, Glover GH, Kenna H, Reiss AL, Greicius MD (2007): Dissociable intrinsic connectivity networks for salience processing and executive control. J Neurosci 27:2349–2356.

Shirer WR, Ryali S, Rykhlevskaia E, Menon V, Greicius MD (2012): Decoding subject-driven cognitive states with whole-brain connectivity patterns. Cereb Cortex 22:158–165.

Sridharan D, Levitin DJ, Menon V (2008): A critical role for the right fronto-insular cortex in switching between central-executive and default-mode networks. Proc Natl Acad Sci USA 105:12569–12574.

Stokes MG, Kusunoki M, Sigala N, Nili H, Gaffan D, Duncan J (2013): Dynamic coding for cognitive control in prefrontal cortex. Neuron 78:364–375.

Uddin LQ, Kinnison J, Pessoa L, Anderson ML (2014): Beyond the tripartite cognition-emotion-interoception model of the human insular cortex. J Cogn Neurosci 26:16–27.

Uddin LQ, Menon V (2009): The anterior insula in autism: Under-connected and under-examined. Neurosci Biobehav Rev 33: 1198–1203.

Vuilleumier P, Driver J (2007): Modulation of visual processing by attention and emotion: Windows on causal interactions between human brain regions. Philos Trans R Soc Lond B Biol Sci 362:837–855.

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

Whalen PJ (1998): Fear, vigilance, and ambiguity: Initial neuroimaging studies of the human amygdala . Curr Dir Psychol Sci 7:177–188.

Zhang W, Luck SJ (2011): The number and quality of representations in working memory. Psychol Sci 22:1434–41.