Probing emotional influences on cognitive control: An ALE Meta-Analysis of cognition emotion interactions

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Abstract

Increasing research documents an integration of cognitive control and affective processes. Despite a surge of interest in investigating the exact nature of this integration, no consensus has been reached on the precise neuroanatomical network involved. Using the Activation Likelihood Estimation meta-analysis method, we examined 43 functional Magnetic Resonance Imaging (fMRI) studies (total number of foci = 332; total number of participants, N =820) from the literature that have reported significant interactions between emotion and cognitive control. Meta-analytic results revealed that concurrent emotion (relative to emotionally neutral trials) consistently increased neural activation during high relative to low cognitive control conditions across studies and paradigms. Specifically, these activations emerged in regions commonly implicated in cognitive control such as the lateral prefrontal cortex (inferior frontal junction, inferior frontal gyrus), the medial prefrontal cortex, and the basal ganglia. In addition, some areas emerged during the interaction contrast that were not present during one of the main effects and included the subgenual anterior cingulate cortex and the precuneus. These data provide new evidence for a network of cognition emotion interaction within a cognitive control setting. The findings are discussed within current theories of cognitive and attentional control.

Keywords: meta-analysis, fMRI, executive function, emotion, affective

Introduction

Contrary to a long tradition of research, increasing evidence suggests that "cold" higher-order cognitive systems and "hot" affective, emotional systems do not operate independent of one another (Gray, Braver et al. 2002, Pessoa 2008, Banich, Mackiewicz et al. 2009, Mueller 2011). Supported by these findings, recent theoretical views have challenged the common assumption of a "modular" view of neural processing, i.e., that emotion on the one hand and cognition on the other hand occupy distinct anatomical areas in the brain (Pessoa 2008). Instead, these theories propose that affective and cognitive mechanisms are processed in shared underlying neurocircuitry (Pessoa 2008, Shackman, Salomons et al. 2011). However, the precise nature of this integration and its underlying neuroanatomy are still unclear.

Cognitive control, a skill commonly associated with 'cold' higher-order processing, is essential for goal-oriented behavior and linked to function of the dorsolateral prefrontal cortex (dlPFC) (Miller and Cohen 2001) and the dorsal anterior cingulate cortex (dACC) (Botvinick, Nystrom et al. 1999). In a first study that examined how emotion and cognitive control integrated, Gray et al. (2002) reported that the dlPFC response during a working memory task was modulated by prior positive or negative mood induction. However, responsivity of cognitive control to emotional material has also been reported in other brain regions including the anterior insula (Levens and Phelps 2010), amygdala (Van Dillen, Heslenfeld et al. 2009), striatum (Padmala and Pessoa 2010), or parietal cortex (Schulz, Clerkin et al. 2009) suggesting a contribution of regions outside the prefrontal cortex in this process. Despite an increase in fMRI work on this topic, no consensus has been reached on the precise neural networks involved in the interaction between cognitive control and emotion. Part of this problem is that different emotional dimensions (e.g., prior mood induction, emotional distraction) have been intermixed with a variety of "classic" cognitive control tasks (e.g, n-back working memory task, the Stroop task, or the go/no-go task)(c.f. Table 1 and Mueller 2011). Yet, knowledge of regions of interaction and integration are theoretically important to define the circumstances under which emotion and cognitive control can conjointly modify behavior or operate in a hierarchical order of processing at both the behavioral and neural level.

As alluded to above, one distinctive problem in the identification of regions of integration is the variability of processes involved. Cognitive control is an umbrella term for a variety of separable executive processes including set-shifting, inhibition, maintenance and updating of working memory, or error monitoring (Banich et al., 2009; Miyake et al., 2000). Emotion, by comparison, is varied in valence (e.g., positive or negative), can occur during (Dolcos and McCarthy 2006, Goldstein, Brendel et al. 2007, Habel, Koch et al. 2007) or prior to (Deckersbach, Rauch et al. 2008, Hart, Green et al. 2010) cognitive control, and can have distinct motivational significance (approach-related vs. avoidance-related) (Sutton and Davidson 1997, Roseman 2008). Inconsistency in findings occurs at several levels. For example, whilst most studies seem to report an increase in the BOLD response during the critical interaction condition (Blair, Smith et al. 2007, Pereira, de Oliveira et al. 2010), other studies have reported a paradoxical signal decrease (Dolcos and McCarthy 2006, Fruhholz, Fehr et al. 2009). Discrepancy also extends to the behavioral outcome of dealing with emotion during a standard cognitive control task. While some authors have reported that concurrent emotion impairs cognitive control (Dolcos and McCarthy 2006, Wessa, Heissler et al. 2012), others suggest a boost of cognitive control performance in the presence of affective material (Fruhholz, Fehr et al. 2009, Kanske and Kotz 2011). A third factor that may impact the integration process is the relevance of the emotion for the current task. In some tasks, the affective dimesion is task-relevant, i.e., participants need to pay close attention to the affective stimulus to solve the task (e.g., Goldstein, Brendel et al. 2007, Chechko, Wehrle et al. 2009). In other studies, the affective dimension was task-irrelevant, i.e., the affective stimulus served as a distractor (e.g., Hart, Green et al. 2010, Wessa, Heissler et al. 2012). These circumstances, alone or in combination, may have so far prevented a transparent picture of how emotion affects critical cognitive control processes. It is thus unclear whether a) the presence of emotion boosts cognitive control due to higher biological significance or whether b) emotion interferes with self-regulatory control, which leads to increased recruitment of cognitive control areas to maintain equilibrium.

This study aimed to clarify these inconsistencies by virtue of a meta-analytic procedure, the Activation Likelihood Estimation (ALE) meta-analysis method (Turkeltaub, Eden et al. 2002, Eickhoff, Laird et al. 2009). Usage of the meta-analysis method has several advantages. First, we wanted to identify consistently activated brain regions during interactions between emotion and cognitive control across tasks and affective dimensions. Second, this identification would provide necessary empirical support across studies for or against current theories of emotion cognition integration (c.f. Gray 2001, Pessoa 2008). Third, a survey of the current literature would identify gaps and engender essential questions in need of pursuit to better characterise integrative processes between the affective and control systems. Of note, given that previous meta-analyses and reviews have examined the cognitive control of emotion (i.e., emotion inhibition, cognitive re-appraisal) (Bush, Luu et al. 2000, Diekhof, Geier et al. 2011), the present study focused selectively on the influence of emotion on ‘cold’ cognitive control, not vice versa. To this aim, a meta-analysis was performed on studies that specifically reported significant interactions between emotion and cognitive control.

Method

Study selection

Relevant studies were identified through a systematic database search for peer-reviewed articles published between January 1995 and September 2012 on ISI Web Of Knowledge (Thomson Reuters, NY, USA) and PubMed. Searches were conducted with the keywords “fMRI” or “functional magnetic resonance”, in combination with one or two of the following search terms:

"emotion", "affective, "reward", "motivation", "cognitive control", "cognitive interference", "emotional interference", "emotion-cognition", "cognition-emotion", "inhibition", "Stroop", "flanker", "go nogo", "stop signal", "task switching" and "working memory". In addition, the reference lists of the selected articles were used to identify additional relevant papers. This search yielded 1347 papers (see Appendix 1 for a flowchart of detailed selection and reasons for exclusion).

Studies were required to fulfill the following criteria for inclusion: 1) Since we were interested in the neural correlates of emotion-cognition interactions only fMRI studies were included; 2) Selected studies had to report [x, y, z] coordinates for interaction effects between emotion and cognitive control in standard stereotactic space (either Talairach or MNI). Studies not reporting specific coordinates were excluded; 3) Only data from experiments in healthy adults were included. However, coordinates from healthy controls in patient studies were also included if separate within-group contrasts were provided; 4) To avoid bias in the data we excluded studies using an anatomical region-of-interest (ROI). Studies performing a whole brain (WB) analysis or functional ROI were included. In total, 43 fMRI studies (total number of foci = 332; total number of participants, N = 820) were included in the final meta-analysis (Table 1). Foci that were located outside the mask of gray matter used by GingerALE 2.1 were excluded from all analyses.

************************ TABLE 1 about here please ***********************

Contrast selection

This study sought to examine how emotion modulates neural activity during cognitive control performance. To this end, studies reporting an interaction between a cognitive control task and an emotional context were selected. However, since statistical interaction effects could be driven by both activations and deactivations, because of the difficulty in interpreting deactivation and because few studies have reported such deactivations, only contrasts of increased activation in the emotional cognitive control condition were included (cf. details of contrast selection per study in Table 1). This inclusion criterion also facilitated interpretation.

In addition to examination of general brain networks involved in emotion cognitive control integration, two additional subanalyses were performed. First, studies were divided into those where emotional stimuli were task-relevant or task-irrelevant, i.e., whether the stimuli needed to be attended to or served as distractors. Second, tasks were separated by their effects in the behavioral data, i.e., whether studies reported improvements or impairments during the emotional condition.

Although comprehensive meta-analyses on cognitive control (Wager and Smith 2003, Wager, Jonides et al. 2004, Derrfuss, Brass et al. 2005) and emotion (Wager, Phan et al. 2003, Shackman, Salomons et al. 2011) in isolation are available in the literature, for the sake of internal consistency and to facilitate comparisons between regions, *main effects* of cognitive control and emotion processing were also computed. Cognitive control contrasts included comparison of the condition with high vs. low control requirements (e.g., incongruent vs. congruent; NoGo vs. Go; task switch vs. task repeat, high vs. low working memory load) either in the neutral condition only or combined across valences. This resulted in 243 foci from 20 experiments. Similarly, for the main contrast of emotion, activation by emotional stimuli were compared to neutral stimuli (positive/negative vs. neutral or reward vs. no reward) collapsed across cognitive control conditions yielding 246 foci from 19 experiments. Of note, the “main effect” of emotion must still be understood within the context of a cognitive control experiment and other studies may be more suitable to identify “pure” emotion circuitry in the absence of a behavioral control task.

ALE analysis

To assess which brain regions were implicated in emotion-cognitive control integration, we used the ALE meta-analytic approach (Turkeltaub, Eden et al. 2002, Eickhoff, Laird et al. 2009) using GingerALE software (version 2.1 www.brainmap.org/ale). Unlike previous meta-analytic methods (e.g. based on anatomical labels or Brodmann areas (BAs)), this method provides a quantitative and objective measure of the convergence of neuroimaging findings. ALE was performed in Talairach and Tournoux (1988) stereotactic space and all coordinates reported in MNI space were converted to Talairach coordinates using the Lancaster transformation (Lancaster, Tordesillas-Gutierrez et al. 2007, Laird, Robinson et al. 2010).

In an ALE-analysis, three-dimensional (Talairach or MNI) activation foci are extracted from relevant contrasts reported in selected neuroimaging studies. These peak activation coordinates are modelled as a three-dimensional Gaussian distribution with an estimated Full-Width Half-Maximum (FWHM) based on the number of participants in the study. Probability distributions within an experiment are merged into a “modelled activation” (MA) map, which reflects the probability for each (2 mm^3) voxel that at least one of the foci is located within that voxel. The individual MA maps are then combined into an ALE-map on a voxel-by-voxel basis, controlling for within-experiment effects (Turkeltaub, Eickhoff et al. 2012). The ALE-map reflects the combined activation patterns across all experiments included in the meta-analysis. To determine statistical significance, the ALE-map is tested against an ALE null distribution map, derived from a permutation procedure. To control for multiple comparisons, the ALE-map was thresholded at a false discovery rate (FDR) of $p<0.05$, corrected. Whereas other recent meta-analyses have commonly used a minimal cluster size of 100 mm^3 (Swick, Ashley et al. 2011, van der Laan, de Ridder et al. 2011, Veldhuizen, Albrecht et al. 2011, Brooks, Savov et al. 2012) we opted to use a slightly more conservative cluster size threshold of 200 mm^3 (c.f. Owen, McMillan et al. 2005, Diekhof, Geier et al. 2011).

ALE-maps were overlaid onto an anatomical T1-weighed image in Talairach space and displayed with Mango software (http://ric.uthscsa.edu/mango/). Anatomical labels were assigned using the Talairach Daemon (http://www.talairach.org/daemon.html) and the Human Brain Anatomy in Computerized Images Atlas (Damasio 2005).

******************** TABLE 2 about here please *******************

Results

Influence of emotion on cognitive control (interaction effect)

The main ALE-analysis of significant interactions between emotion and cognitive control revealed 18 significant clusters (Table 2, Figures 1, 2), with the largest cluster (volume = 3960 mm^3) located in the medial and superior frontal gyrus (BAs 6/32). The maximum ALE value of 0.031 was observed in the right inferior frontal gyrus (IFG; cluster volume = 2488 mm^3). Other clusters included the right dlPFC (BA9), left IFG (BA 6), anterior insula, inferior parietal cortex (IPC), and bilateral subgenual anterior cingulate cortex (ACC; BA 25). In addition, activation was also found in subcortical regions such as the right amygdala.

****************** FIGURE 1 about here please ********************

Emotion-cognition interaction: the use of task-relevant vs. task-irrelevant emotional stimuli

An additional analysis was conducted to disentangle findings from studies in which emotional stimuli were relevant to the task and required attention or were irrelevant and served as distractors. When emotion was task-relevant (N = 19 studies, 161 foci), prominent clusters emerged in the medial and superior frontal gyrus (BA6), right putamen, bilateral subgenual ACC

(BA25), bilateral fusiform gyrus (BA19/37), and medial globus pallidus (Figure 3, orange clusters). When emotion was task-irrelevant (N = 14 studies, 112 foci), significant clusters emerged in the medial and superior frontal gyrus (BA 32), right dlPFC (BA9) and bilateral IFG (BA 6). Other clusters were located in the right amygdala, left insula, left inferior parietal lobule (IPL; BA 40) and right superior parietal lobule (SPL; BA 7) (Table 3 and Figure 3, purple clusters). To directly contrast both types of tasks, task-relevant activation clusters were subtracted from task-irrelevant activation clusters. Here, two interesting clusters were significant in the right dlPFC (BA 9; cluster volume = 816 mm^3) and IPL (BA 40; volume = 288 mm^3), implying that these areas were activated more if emotion was task-irrelevant as opposed to task-relevant. The reverse subtraction yielded no significant findings.

************************FIGURE 2 about here please ***************

********************** TABLE 3 about here please ******************

Emotion-cognition interactions resulting in impaired vs. improved performance

The second additional analysis sought to discriminate between studies that have reported either improved or impaired behavioral performance during the emotion condition of a cognitive control task. When the emotional manipulation resulted in improved performance (N = 10 studies, 52 foci), a large cluster in the superior frontal gyrus emerged (BA 6; volume = 1208 mm^3; ALE-value = 0.0183). Other activations were located in the right IFG(BA 9), right hypothalamus, right caudate body and right angular gyrus (BA 39) (Table 4 top; Figure 3, green clusters). In studies where the presence of emotion impaired cognitive control (N = 14 studies, 121 foci) the largest and most significant cluster was also located in the superior frontal gyrus (BA 6; volume = 1248 mm^3). Additional clusters were found in the left occipital gyrus (BA 17), bilateral precuneus (BA 7/31), right fusiform gyrus (BA 19), right subgenual ACC (BA 25), left IFG (BA 45) and left amygdala (Table 4 bottom; Figure 3, red clusters). A direct statistical comparison of studies reporting improved and impaired performance yielded no clusters.

************************FIGURE 3 about here please ***************

********************** TABLE 4 about here please ******************

Main effects of cognitive control and emotion

The meta-analysis of the main effects of cognitive control and emotion were conducted for easier comparison and served as internal control contrast. The main effect of cognitive control in the absence of emotion revealed 17 clusters. The highest ALE-scores and largest clusters were located in the bilateral insula (volume left = 1952 mm^3; ALE-value left = 0.0441; volume right = 3104 mm^3; ALE-value right = 0.0358), bilateral IFG (BA9; volume left = 2448 mm^3; volume right = 744 mm^3; ALE-value left = 0.0319; ALE-value right = 0.0224) and medial frontal gyrus (BAs 6/8; volume = 4448 mm^3; ALE-value = 0.0276). Other clusters were located in the bilateral supplementary motor area (SMA), bilateral SPL and right dlPFC (Figure 2, Appendix 2 top).

For regions activated during affective processing in the absence of a cognitive control condition, 13 significant clusters emerged. These local maxima emerged in several regions including the bilateral amygdala, superior temporal gyrus, insula, and medial ACC (Figure 2, Appendix 2 bottom).

Discussion

This meta-analysis aimed to provide an objective overview of, and synthesize, discrepant findings on the influence of affective processing on cognitive control. Four main findings pertinent to the study goal emerged. First, several brain regions at both the cortical (e.g., IFG, dlPFC, IPL, subgenual ACC) and subcortical level (anterior insula, putamen, and amygdala) consistently responded to an emotional challenge within a cognitive control setting. Second, this analysis revealed two regions involved in the integration of emotion and cognition, i.e., a presence in the interaction but not in the main effects analysis, namely the bilateral subgenual ACC and the precuneus. Third, tasks where emotional stimuli served as distractors yielded increased activation in dlPFC and parietal cortex compared with tasks where emotion was relevant for the task at hand. Fourth, analyses also showed that behavioral performance patterns were associated with both similar and distinct regions. While activity in the superior frontal gyrus was increased irrespective of performance, clusters in 'emotional' regions (e.g. amygdala, subgenual ACC) were only found if performance was impaired. However, the direct contrast between improved and impaired performance did not reveal any significant regions.

ALE meta-analysis of increased activation during emotion-cognition interactions

The interaction analysis revealed many clusters that are traditionally associated with both cognitive control (e.g. IFG, dlPFC) or emotion processing (e.g. amygdala, insula, striatum, subgenual ACC). Within the lateral PFC two clusters were identified, i.e. right dlPFC and inferior frontal junction (IFJ). Traditionally, the dlPFC is associated with maintaining the representation of task goals in working memory (Miller and Cohen 2001). A previous meta-analysis of studies on set-shifting tasks, response reversal tasks, and Stroop paradigms has specifically implicated the IFJ, an area located within the vicinity of the junction between the inferior frontal and inferior precentral sulci of the lateral prefrontal cortex (PFC), in the updating of task representations (Derrfuss et al., 2005). At the exact same coordinates as reported by that earlier meta-analysis, we not only found a main effect of cognitive control (thus independently replicating Derrfuss et al.'s finding in a different set of studies) but importantly showed that this region has an intimate relationship with emotional processes. Such data suggests that emotional material modulates the updating of task representations in the lateral PFC. It is conceivable that additional recruitment of this region in the presence of emotion could reflect increased updating of task goals to counteract the deleterious influence of emotional distractors on cognitive control. Likewise, consistent with a role of the right IFG in inhibition (Aron, Robbins et al. 2004), increased responding of this region in the presence of emotion could mirror suppression of the emotional material to prioritize the executive task. However, significant interaction between emotion and cognitive control was not restricted to the lateral PFC.

Previous work has focused on the anterior midcingulate cortex (aMCC) as a potential site of integrating negative affect and cognitive control (Shackman, Salomons et al. 2011). These authors suggest that the aMCC executes control in case of uncertainty of action. The present findings in posterior medial frontal cortex (pMFC) corroborate these suspicions but extended findings of interaction to regions beyond the frontal cortex. One such region was located in the IPC) and within the bank of the angular gyrus [hlP1, human intraparietal area 1, (Choi, Zilles et al. 2006)] as well as the anterior insula cortex (AIC). The IPC is attributed to be part of a fronto-parietal attention network, where it contributes to reorienting attention to task-relevant stimuli (Corbetta and Shulman 2002, Liu, Banich et al. 2004). In an interesting recent proposal, hlP1 projects to the anterior insula cortex (AIC) via the dorsal visual pathway (Uddin, Supekar et al. 2010). There, the AIC detects the saliency of a stimulus and engages distributed attentional and higher-order control processes (Menon and Uddin 2010). Consistent with these models of a parietal attention network (Corbetta and Shulman 2002) and anterior insula function (Menon and Uddin 2010), the presence of these areas in the current analysis suggests that emotional material modulates this cascade process of attentional processing. However, it is unclear whether presence of affective material receives preferential processing due to high salience or, alternatively, whether detection of the presence of salient material by the AIC engages additional control resources (e.g., dlPFC, ACC) to compensate distraction. Future work will need to address this issue.

A second finding of the meta-analysis revealed two regions, the bilateral subgenual cingulate and the dorsal posterior cingluate (dPCC)/precuneus, that were only significant during the interaction contrast but that did not emerge in either the cognitive control or emotion contrast alone. Although previous authors have suggested a special role of regions activated only in integration contrasts but not main effects (Gray, Braver et al., 2002), the present findings are ambiguous in that sense. For example, although the subgenual ACC did not appear in a main effect of emotion in the present study, this might be, to some extent, related to the fact that the analyses were conducted within a cognitive control background. In any case, the subgenual ACC has been identified as a major player in mood disorders, particularly depression (Drevets & Raichle, 1998) with strong projections to visceral and emotional control centers (Freedman, Insel et al. 2000, Drevets and Savitz 2008). Similarly, the dPCC (BA31) has also been implicated in mood disorders (Price and Drevets 2010) and the precuneus (BA7) participates in episodic memory and self-referential processing (Cavanna and Trimble 2006). Unfortunately, given the cluster size of the present activation and overlap among Brodmann areas, a precise distinction between the dPCC and precuneus cannot be made at this point. Given that the present results are located more laterally, they are consistent with functional connectivity studies that have suggested intrinsic functional connections with cognitive and visual areas (Margulies, Vincent et al. 2009). Taken together, these meta-analytic data suggest that the subgenual ACC and dPCC/precuneus may play a role in integrating affective processing with cognitive control in areas with links to visceral control anteriorily and cognitive and visual processing posteriorily. However, several factors are likely to modulate this processing such as the relevance of the emotional material to the task and/or the resultant effect on behavioral performance.

The impact of task-relevance on cognition-emotion interactions

Indeed, when emotional stimuli were relevant to the task and required attention, increased activation in visual areas (fusiform gyrus and primary visual cortex) and the subgenual ACC became apparent. Activation in visual areas could reflect prioritized processing of the salient, high-arousing emotional information (Mather et al., 2006). Given the subgenual ACC's strong links to both emotion centers (i.e., amygdala; Freedman, Insel et al. 2000) and visceral control centers (i.e., the hypothalamus, periacquaductal grey, and paraventricular nucleus of the thalamus) (Price and Drevets 2010), this activation could reflect inhibition or suppression of emotion processing (e.g., Goldstein et al., 2007; Kanske & Kotz, 2011). By contrast, when emotional stimuli were task-irrelevant and merely served as distractors to the cognitive control task, activation clusters were found in both cognitive (dlPFC, IFJ, Me/SFG, IPL, SPL) and affective (insula, amygdala) regions. Of note, particularly activation in the right dlPFC and the IPL was increased in the irrelevant condition when directly compared to the relevant condition. Additional recruitment of these regions when emotion is irrelevant might reflect their role in counteracting the distracting effect of emotional stimuli by increasing task-specific activity (Wessa et al., 2012). By comparison, given that no differential activity between relevant and irrelevant stimuli emerged in affective regions during the direct contrast, limits interpretation of emotional neurocircuitry during the processing of task relevance. In any case, if increased activity in cognitive control regions is indeed reflecting allocation of processing resources to task-relevant information, this activity should be related to performance improvements at the behavioural level. On the other hand, if additional recruitment of cognitive control regions is related to performance impairments, this increased activity could reflect efforts to inhibit the emotional information, thus depleting processing resources that would otherwise have been allocated to the task.

The impact of task-performance on cognition-emotion interactions

Additional subanalyses on studies showing either performance improvement or impairment were carried out in order to evaluate both accounts. When performance was improved, consistent activation was limited to frontal regions (SFG and right IFJ) and the angular gyrus with no clusters in ‘affective’ regions. Activity in these regions presumably reflects increased task-specific activity and the recruitment of the fronto-parietal attention network to reorient attention to goal-relevant information. By contrast, when concurrent emotion impaired performance, activation clusters were found in both frontal (e.g. inferior, medial, and superior frontal gyrus) and limbic (e.g. amygdala, subgenual ACC) regions. This finding supports the idea that the inhibition of emotional information consumes processing capacity, diminishing the available resources for task-relevant processing and resulting in impaired performance. Although a dissociation between frontal regions and performance improvement on the one hand and frontal and limbic regions and performance impairment on the other hand is tempting, interpretation is limited given that no clusters emerged in the direct contrast between improvements and impairments. Direct comparisons of improved vs. impaired behavioural performance, possibly on a trial-by-trial basis, might reveal a link between behavioural outcome and limbic recruitment.

Future directions and limitations

A last goal of this study was to identify gaps for further enquiry. Most of the included studies compared negative to neutral stimuli (N = 32 studies), while fewer studies looked at positive emotions (N = 13 studies). A differential impact of positive and negative valence on behavioral control seems plausible, given hypothesised hemispheric-specific processing in approach and avoidance-related behavior (Sutton and Davidson 1997). Thus, future work should investigate neurobiological evidence for theoretical models of positive emotion on cognitive control processes and executive attention (Ashby, Isen et al. 1999). In addition, given the multitude of paradigms reported in the literature, we could not disentangle contributions by specific executive processes and tasks. However, the purpose of this meta-analysis was to identify similarities across studies within the domain. Future work can assess in more detail the influence of task and process-specific effects on cognition-emotion interactions. Similarly, given that only a minority of studies reported deactivations, a more detailed analysis of the processes underlying these deactivation was not possible and should be taken into consideration in future research.

Conclusion

In summary, this meta-analysis sought to find consistencies among an increasing number of studies investigating the influence of emotion on cognitive control. Increased neural activity during affective processing whilst performing a cognitive control task resulted in activation of a range of cortical and subcortical areas. However, these activations were partly modulated by task relevance of the affective stimulus and behavioral outcome suggesting that these factors should be taken into account when interpreting findings. Importantly, the results highlight two regions that were unique to the interaction contrast, the precuneus and the subgenual ACC. Future work is needed to define the precise functional contribution of each structure and clarify theoretical views on integrative processing.

Acknowledgements

We acknowledge the support of Ghent University (Multidisciplinary Research Partnership “The integrative neuroscience of behavioural control”). We would also like to thank the two anonymous reviewers and Marcel Brass for valuable suggestions on an earlier version of this manuscript.

Conflict of interest

The authors declare that they have no conflict of interest.

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Figure captions

Fig. 1 Significant activations during the interaction between emotion and cognitive control are presented on underlying anatomical T1 axial slices. ACC = anterior cingulate cortex ; IFJ = inferior frontal junction; dlPFC = dorsolateral prefrontal cortex; pMFC = posterior medial frontal cortex. x, y, z coordinates are reported in Talairach space. Image activations were thresholded at p<.05 FDR. Strength of activation reflected by brightness of respective colour.

Fig. 2 Significant activations of interaction (red color) overlaid with the main effects of cognitive control (green color) and emotion (blue color). Image activations were thresholded at p<.05 FDR.

Fig. 3 The figure shows significant activations as a response to task-relevant (orange color) and task-irrelevant (purple color) emotional stimuli. In addition, the figure also depicts the significant activation clusters for impaired (red color) and improved (green color) performance. x, y, z coordinates are reported in Talairach space. Image activations were thresholded at p<.05 FDR.

FIGURE 1.

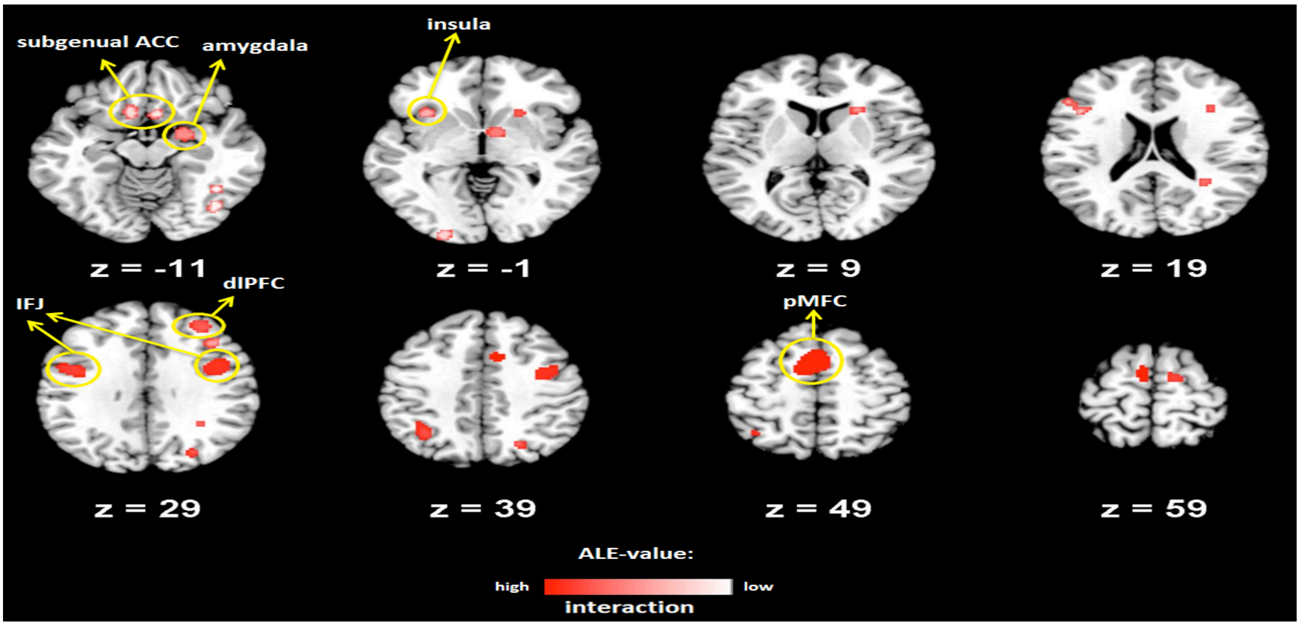


FIGURE 2.

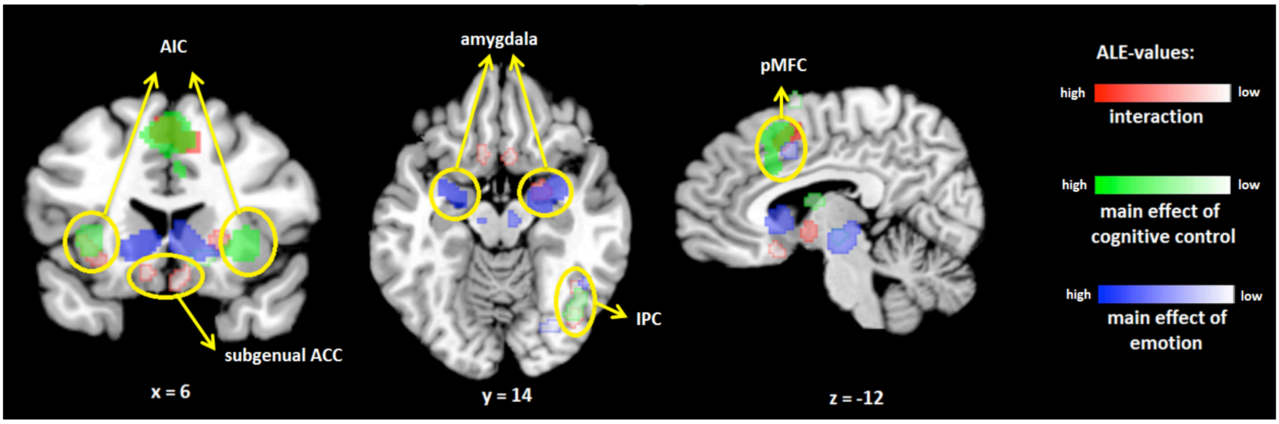


FIGURE 3.

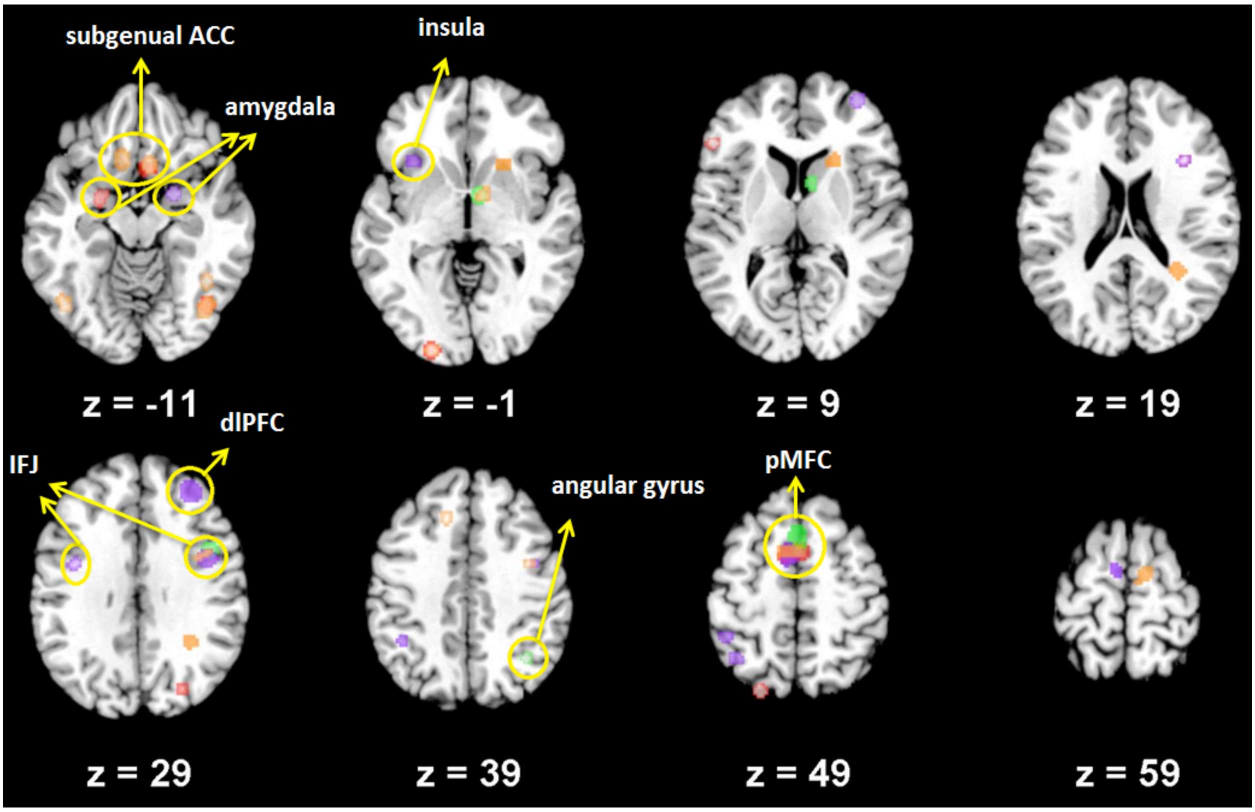

subgenual ACC
insula
amygdala
z = -11
z = -1
z = 9
z = 19
dlPFC
IFJ
angular gyrus
pMFC
z = 29
z = 39
z = 49
z = 59

Table 1. Overview of studies included in the meta-analysis

First Author	*Year*	*n*	*Experimental Paradigm*	*Emotional Stimuli*	*Behavioural interaction effect*	*Experimental contrast*
Beck	2010	31	delayed item recognition WM	liquid vs monetary reward	ME incentive condition (Money/Liquid > Baseline) during WM task	incentive > baseline during WM task
Beneventi	2007	12	1- and 2-back WM task	(scrambled) drawings of facial expressions	ns	facial expressions > scrambled drawings during n-back task
Blair	2007	22	modified affective stroop	IAPS (neg, pos, neu)	ns	negative (incongruent vs view) > neutral (incongruent vs view); positive (incongruent vs view) > neutral (incongruent vs view)
Brown	2012	20	emotional go-nogo task	IAPS (neu, aversive)	ns	(Aversive NoGo - Aversive Go) - (Neutral NoGo - Neutral Go)
Chechko	2009	18	emotional Stroop task	happy/fearful faces	-	emotionally incongruent > emotionally congruent (in controls); D: emotionally congruent > emotionally incongruent (in controls)
Chechko	2012	24	emotional Stroop task	happy/sad/fearful faces	task x congruency, F(1, 23) = 20, p < .001; stronger interference effect in the emotional vs non-emotional task	emotional (incongruent > congruent) - non-emotional (incongruent > congruent); D: non-emotional (incongruent > congruent) > emotional (incongruent > congruent)
Deckersbach	2008	17	2-back WM task	mood induction (autobiographical scripts)	RT in 2-back: no mood induction < neutral state induction < negative state induction	sad > neutral during 2-back task
Dolcos	2006	15	delayed WM for faces with emotional scene distraction	IAPS plus in-house	ME of distracter type (worse performance for emotional compared to neutral and scrambled distractors)	Emo > Scram, Emo > Neu; D: Scram > Emo, Neu > Emo
Dolcos	2008	14	delayed WM for faces with emotional face and scene distraction	IAPS plus in-house	ns	neg > face, neg > neu and scramb face > face during WM task; D: face > neg, face > scramb face
Erk	2007	12	item recognition task (low vs high load), IAPS during delay	IAPS (neg, pos, neu)	no load x valence interaction; within load 6: better performance during positive, negative and no picture vs neutral condition	negative (load1+6) > neutral (load 1+6) inclusively masked with load 6 (neg+neu)>load1(neg>neu)

Fruehholz	2009	20	forced-choice categorization of neg, neu and pos expressions with conflicting background (based on previous run)	neg, pos, neu faces	significant emotion x congruence interaction (F = 4.46; p = .018); stronger increase in RTs for incongruent trials with neutral expressions	negative (incongruent > congruent) > neutral (incongruent > congruent) + positive (incongruent > congruent); D: incongruent neutral > incongruent negative/positive
Goldstein	2007	14	go no-go emotional linguistic	neg, pos, neu words	RT significantly slower in no-go vs go within negative and positive valence condition, and trend within neutral valence	[(NegNoGo - NegGo) - (NeuNoGo - NeuGo)] and [(PosNoGo - PosGo) - (NeuNoGo - NeuGo)]
Gray	2002	14	emotional induction (short videos) followed by 3 back task	verbal and non verbal	word 3-back enhanced by pleasant state and impaired by unpleasant state, wherease face 3-back showed the reverse effect	integration-sensitive regions
Habel	2007	21	n-back WM task during neg. olfactory stimulation	letters, rotten yeast smell	olfactory stimulation x task interaction: F(1, 19) = 6.98; p = .02; RT 2-back neg > neu in AG	(2-back yeast masked with 0-back yeast) vs (2-back air masked with 0-back air)
Hart	2010	14	emotional priming during number stroop	IAPS (aversive, neutral)	emotionality x Stroop content: F(2,12) = 3.99; p = .047; slower RT on incongruent trials when preceding aversive vs. neutral stimulus	aversive incongruent > neutral incongruent
Kanske	2011	20	colour flanker task	neg, neu words	emotion x conflict: F(1,19) = 4.6; p < .05; reduced conflict for neg vs neu trials	negative (incongruent vs congruent) - neutral (incongruent vs congruent)
Kanske	2010	22	modified Simon task with emotional and neutral words	neg, pos, neu words	significant emotion (emotional, neutral) x conflict (congruent, incongruent) interaction; F(1,22) = 4.8; p < .05)	negative (incongruent vs congruent) - neutral (incongruent vs congruent)
Kellermann	2011	36	motor short-term memory task with emotional interference	IAPS (neg, pos, neu)	significant picture context (neu, pos, neg picture, green dot) x sequence length (4 or 6 items) interaction	emotion: 6 item > 4 item; emotional pictures (easy > difficult task) > neutral pictures (easy > difficult task)
Kouneiher	2009	16	contextual and episodic control task with low or high incentive	letters, monetary reward	-	contextual and episodic motivation with high vs low incentive
Krebs	2011	18	reward-modulated Stroop	color-words, monetary reward	ns	incongruent reward > incongruent no-reward
Krebs	2012	11	cued-attention paradigm (easy/hard) under reward and no reward	monetary reward	significant reward (reward, no-reward) x difficulty (easy, hard) interaction; F(1,13) = 9.05; p = .01; reward-related RT decrease more pronounced for easy targets	reward x difficulty interaction (high difficulty reward condition > other types)
Lee	2008	14	emotion expression interference task	dynamic facial expressions	-	incongruent - congruent during emotional interference task

Li	2009	33	stop-signal task	-	-	risk taking (RT decrease in post go go-trial) vs risk aversion (RT increase in post go go-trial)
Lim	2008	21	faces with superimposed letter arrays/ high load and low load, selective conditioning to some faces preceded experiment	neu, fearful faces	ns	easy fearful THREAT > SAFE; D: hard fearful THREAT < SAFE
Malhi	2005	12	emotional Stroop task	neg, pos, neu words	-	affective Stroop (neg+pos) > neutral Stroop
Mather	2006	26	emotional source-monitoring task	IAPS (high/medium/low arousal, pos/neg)	significant arousal induced impairment in source memory; F (1,15) = 10.16, p < .05	emotional > neutral; D: neutral > emotional (during WM task)
Melcher	2011	14	Stroop oddball task	IAPS (neg, neu)	trend for a cognitive and emotional manipulation; F(26, 2) = 3.212, p = .057	negative incongruent vs baseline
Mitchell	2006	28	lexical decision task	sentences with emotional content and prosody	significant effect of task condition: accuracy incongruent semantic condition < prosody-only condition; F(1, 27) = 194.72; p < .001	incongruent emotion > prosody only
Mittershiffthaler	2007	17	emotional Stroop task	sad, neu words	RT sad > neu words	negative Stroop > neutral Stroop
Mohanty	2005	17	emotional Stroop task	pos, neg, neu words	-	negative Stroop > neutral Stroop
Mullette-Gillman	2011	20	monetary oddball task	gain/loss	-	reward > no reward; D: no reward > reward (during oddball task)
Ochsner	2008	16	affective and cognitive versions of the flanker task	neg, pos, neu words	ns	incongruent > congruent during affective flanker
Padmala	2011	50	response conflict task under reward and no reward	monetary reward	significant motivation (reward, no reward) x congruency (neutral, congruent, incongruent) interaction; F (2, 98) = 12.11; p < .001	[(incongruent - neutral) during reward - (incongruent - neutral) during no reward]; D: [(incongruent - neutral) during no reward - (incongruent - neutral) during reward]
Park	2008	14	emotional Stroop task	in house (pos, neg)	significant interference effect of emotional incongruence	incongruence > congruence; D: congruence > incongruence (during emotional Stroop)
Pereira	2010	11	target detection task	IAPS and in house (neutral and	slower RT for target detection trials during unpleasant vs neutral blocks (p < .05)	unpleasant > neutral detection

				unpleasant)		
Pochon	2002	6	n-back task under reward and no reward	monetary reward	ns	common activation of WM and reward; D: no reward > reward, inclusively masked with WM
Sagaspe	2011	12	stop-signal task	fearful, neu faces	significant emotion (neutral, fearful) x response condition (Go, StopRespond) interaction; F(1, 11) = 11.29; p = .006; RT StopRespond (failed stop) fearful > neu	StopInhibit Fear > StopInhibit Neutral
Savine	2010	16	task switching (gender:m/f or word: 1 or 2 syllables)	monetary reward	significant incentive x task-switching interaction; F(1, 15) = 11.38; p < .001	incentive x task-switching (incentive cue facilitation during task-switching > single task)
Schulz	2009	24	emotional go-nogo task	happy, sad, neu faces	trend for a ME of face emotional valence on correct inhibitions on no-go trials (happy/sad > neutral); F(2, 46) = 2.73; p = 0.08;	no-go > go in response to emotional faces
Taylor	2004	12	object-WM task with low or high load under reward and no reward	monetary reward	ns	high reward (high - low load) > low reward (high - low load)
VanDillen	2009	17	IAPS interspersed with simple (low load) or hard (high load) arithmetic problems	IAPS (neg, neu)	-	negative (complex > simple); D: negative (simple > complex)
Wessa	2012	30	arithmetic task with emotional distractors	IAPS (neg, pos, neu)	longer RT for emotional vs neutral distractor trials; F(1, 29) = 14.1; p < .001	arithmetic emotional - arithmetic neutral
Wingenfeld	2009	20	emotional Stroop task	neutral, general negative and individual negative words	RT individual negative words > neutral/general negative words	negative Stroop > neutral Stroop

ns = not significant; - = information not available; RT = reaction time; WM = working memory; A = activation; D = deactivation; neg = negative; neut = neutral; pos = positive

Table 2

ALE activation clusters associated with cognition emotion interactions, overlap with the main effect analyses, and regions of true integration

			interaction					main effect of cognitive control				main effect of emotion			
					peak				peak				peak		
L/R	Anatomical label	BA	volume (mm^3)	ALE value (x 10^{-3})	x	y	z	ALE value (x 10^{-3})	x	y	z	ALE value (x 10^{-3})	x	y	z
R	inferior frontal gyrus	6/9	2488	31	40	4	30	26,2	42	4	28	15,5	42	2	30
L/R	superior frontal gyrus/medial frontal gyrus	6/32	3960	28	0	10	48	32	2	14	48				
R	dorsolateral prefrontal cortex	9	704	24,8	32	40	28	21,1	36	38	28				
R	amygdala		512	22,1	22	-2	-10					37	22	-8	-10
L	inferior frontal gyrus	6	904	20,6	-40	0	30	36,7	-44	4	28				
L	occipital cortex (V1/V2)	17	344	20	-20	-92	0								
R	medial globus pallidus		536	19	8	-2	-2					23	14	8	-2
R	putamen		496	18,7	20	16	4	16,1	14	12	-4	23	14	8	-2
L	inferior parietal lobule	7	840	18,5	-34	-56	44	24,8	-26	-58	46				
R	medial frontal gyrus	6	544	18,2	14	-6	56	26,7	26	-2	56				
L	subgenual ACC	25	312	17,6	-8	16	-10								
R	fusiform gyrus	37	200	17,2	40	-52	-12	15,8	38	-66	-12	24,5	42	-48	-16
L	insula		448	17,1	-30	16	-2	50,3	-32	20	2	17,2	-34	26	2
R	fusiform gyrus	19	256	17	40	-66	-10	15,8	38	-66	-12	24,5	42	-48	-16
R	precuneus	7/31	552	16,7	26	-74	26								
R	dorsolateral prefrontal cortex	9	464	16,1	38	26	28	21,1	36	38	28				
R	subgenual ACC	25	256	15,3	6	14	-12								
L	inferior frontal gyrus (pars triangularis)	45	384	14,8	-48	26	20	31,9	-44	6	28				

*Note: all activations FDR corrected p<.05

Table 3. Interaction analyses for studies where emotional stimuli are task-relevant vs. task-irrelevant

L/R	Anatomical label	BA	Peak voxel coordinates			Cluster size (mm³)	ALE value (x 10^{-3})
			x	y	z		
task-irrelevant emotional stimuli							
R	dorsolateral prefrontal cortex	9	30	40	30	1096	24,2
R	inferior frontal junction	6	40	2	28	784	20,0
L	medial/superior frontal gyrus	32	-6	8	44	1488	14,6
R	orbitofrontal cortex	10	36	54	8	312	14,4
R	amygdala		22	-2	-12	264	13,2
L	inferior frontal junction	6	-38	-2	32	264	12,8
R	superior parietal lobule	7	22	-62	54	240	12,6
L	inferior parietal lobule	40	-36	-56	46	256	12,1
L	insula	13	-32	18	2	432	11,8
L	inferior parietal lobule	40	-42	-44	48	376	11,3
R	middle frontal gyrus	6	42	0	44	200	11,2
task-relevant emotional stimuli							
R	putamen		20	16	4	760	18,6
R	fusiform gyrus	19	40	-66	-10	496	17,0
L	primary visual cortex	17	-20	-92	0	272	16,4
R	fusiform gyrus	37	40	-52	-12	256	15,9
L	medial/superior frontal gyrus	6	-8	6	52	736	15,8
R	medial globus pallidus		10	-2	2	360	15,7
L	subgenual ACC	32	-8	18	-10	408	15,6
R	medial/superior frontal gyrus	6	12	-6	56	512	15,6
R	subgenual ACC	25	8	16	-10	312	14,2
L	fusiform gyrus	37	-42	-64	-10	304	13,9
L	medial frontal gyrus	8	-12	26	42	216	13,2
R	inferior frontal junction	6	36	-2	36	296	11,6
contrast: task-irrelevant – task-relevant							
R	dorsolateral prefrontal cortex	9	26	44	28	816	
L	inferior parietal lobule	40	-40	-44	46	288	
contrast: task-relevant – task-irrelevant							
No clusters found							

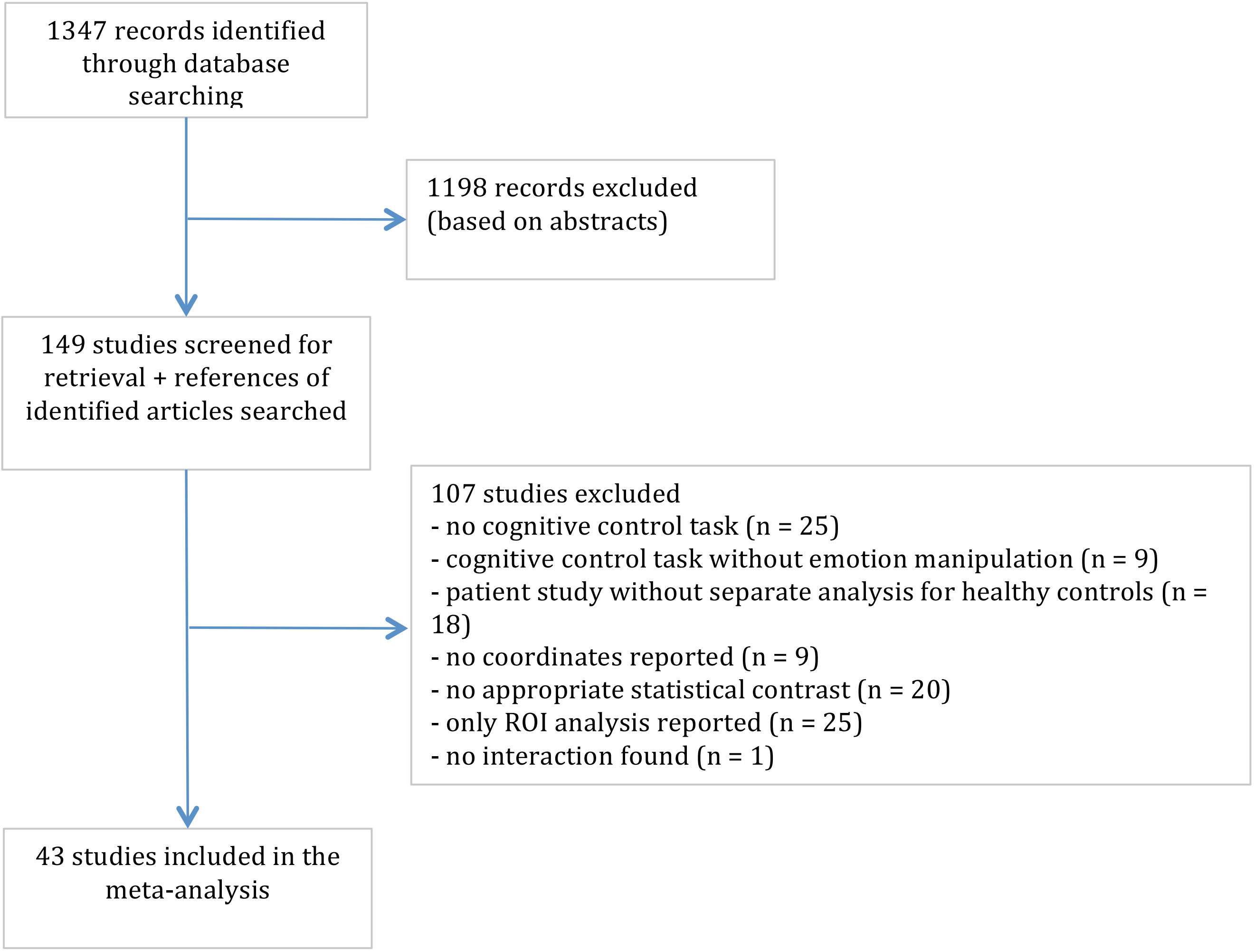
Table 4. Interaction analyses for experiments resulting in impaired and improved performance

L/R	Anatomical label	BA	Peak voxel coordinates x	y	z	Cluster size (mm³)	ALE value (x 10^{-3})
improved performance							
L/R	superior frontal gyrus	6	0	12	50	1208	18,3
R	inferior frontal gyrus	9	42	7	30	480	17,3
R	hypothalamus/medial globus pallidus		6	-2	-2	368	12,8
R	caudate body		8	4	12	288	12,1
R	angular gyrus	39	34	-56	36	224	10,5
impaired performance							
L/R	medial/superior frontal gyrus	6	2	6	50	1248	17
L	occipital gyrus	17	-20	-92	0	408	16,5
R	precuneus	31	26	-74	26	296	16,1
R	fusiform gyrus	19	40	-66	-10	328	15,1
R	subgenual ACC	25	4	14	-14	464	13,8
L	inferior frontal gyrus	45	-48	28	8	232	12,5
L	precuneus	7	-22	-74	50	256	12,4
L	amygdala		-22	-2	-12	296	12,3
L	medial frontal gyrus	6	-8	4	52	1248	11,5

Contrast: impaired – improved performance
No clusters found

Contrast: improved - impaired performance
No clusters found

Appendix 1: Flow chart of the selection process:



Supplementary Table 1. Main effect analyses

L/R	Anatomical label	BA	Peak voxel coordinates			Cluster size (mm³)	ALE value (x 10^{-3})
			x	y	z		
			Cognitive control				
L	insula	13	-32	18	2	1952	44,1
R	insula		32	20	0	3104	35,8
L	inferior frontal gyrus	9	-44	6	28	2448	31,9
L/R	medial/superior frontal gyrus	6	2	14	48	4448	27,6
R	superior parietal lobule	7	32	-54	40	1992	25,1
L	superior parietal lobule	7	-26	-58	46	1784	24,7
R	inferior frontal gyrus	9	42	4	30	744	22,4
R	supplementary motor area	6	26	-2	54	728	21,8
R	dorsolateral prefrontal cortex	9	36	36	30	824	19,3
L	inferior parietal lobule	40	-42	-42	40	632	18,5
R	caudate		10	-8	14	704	17,5
L/R	red nucleus		4	-16	-4	440	16,8
R	putamen		14	12	-4	424	16,1
R	fusiform gyrus	19	38	-66	-12	688	15,8
L/R	superior frontal gyrus	6	6	6	64	264	15,8
L	supplementary motor area	6	-28	-6	54	416	15,2
R	cuneus/occipital gyrus	18	26	-90	0	528	14,9
			Emotion				
R	amygdala		22	-8	-10	3552	31,4
L	amygdala		-10	10	2	2584	28,4
R	putamen		14	8	-2	1912	22,9
L/R	red nucleus		6	-16	-8	408	21,4
L/R	medial ACC	32	6	8	40	808	20,4
R	fusiform gyrus		44	-48	-18	288	20,2
L	precentral gyrus	6	-30	-10	50	944	17,1
R	IPL/precuneus	7/40	32	-52	44	264	16,4
L	middle occipital gyrus	19	-46	-70	8	208	15,9
R	superior temporal gyrus	38	30	4	-30	240	15,2
L	IFG/insula	45	-34	26	4	240	15,2
R	declive		28	-72	-12	408	14,8
L	occipital	18/19	-36	-78	-4		14,6