Neural correlates of error processing:
An ALE meta-analysis

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Abstract

The neural correlates of error processing have been investigated by many neuroimaging studies on interference tasks. Furthermore, it has been suggested that the network processing errors is part of a wider network responsible for conflict monitoring. By using Activation likelihood estimation meta-analysis the aim of this thesis was to delineate regions constantly involved in error processing and compare these regions to those involved in conflict monitoring. Therefore, a total of 38 experiments probing error processing in healthy subjects were included in the main analysis. Results revealed a network for error processing containing the anterior cingulate cortex (ACC) extending into the left superior medial gyrus (SMG) and the left pre-supplementary motor area (pre-SMA), as well as the left and right anterior insula (aI) extending into the right inferior frontal gyrus (IFG) and the bilateral supramarginal gyrus and the left dorsolateral prefrontal cortex (DLPFC). Performing a conjunction analysis across these results with those of a meta-analysis across conflict monitoring revealed conjoint activity of the anterior midcingulate cortex (aMCC) extending into the pre-SMA as well as the bilateral aI and the right supramarginal gyrus. Compared to the network of conflict monitoring stronger significant convergence across studies was found for error processing in the rostral ACC, the bilateral aI lying more lateral than the effect found in the conjunction analysis and the bilateral supramarginal gyrus, for the right supramarginal gyrus lying more lateral than the effect found in the conjunction. Taken together these results provide evidence for the hypothesis that there is not a specific network for error processing, but rather argue for a more general, unitary system for monitoring of cognitive conflict that also involves error monitoring.

Neural correlates of error processing: an ALE meta-analysis

Errors play a big role in our everyday life: they have an influence on our attention (Posner & Petersen, 1990), on learning processes (Ullsperger & von Cramon, 2004), and on emotions like frustration (Taylor et al, 2007). When talking about errors it is important to first define what is meant with this term. One short but appropriate definition is the one of Leape (1994), who defined an error as “an unintended act (either of omission or commission) or one that does not achieve its intended outcome”. Errors often lead to changes in behavior afterwards. An example of changes in behavior after committing an error is that people tend to react more slowly and accurate afterwards, what is called *post-error slowing* (PES). The most common and confirmed explanation for PES is that committing an error increases cognitive control processes and makes people become more cautious than after a correct trial (Dutilh et al., 2012). There are also studies that found the opposite result, that people become less cautious in the following trials, after making an error. These latter studies have in common that they have a very short inter-trial interval leading to the suggestion that in these conditions people can not adapt their behavior as they do not have enough time to process the outcome and adjust their behavior accordingly (Wessel, 2018). This is in line with the finding that the PES only arises, when the subject is aware of having made an error (Klein et al., 2007). While PES can be seen as immediate error correction, errors can also lead to long-term adjustment for similar situations in the future (Ullsperger & von Cramon, 2004). For example, a person who crashed his car due to the fact that he confounded forward- and reversing gear, in the future may be more attentive to the gear change before using the gas pedal.

The most replicated finding to analyze the influence of errors on brain activity is the error-related negativity (ERN), also called error negativity (Ne) using EEG. The ERN is an event-related potential, with a sharp negative wave that peaks approximately 50-100 ms after committing an error and has a distinct amplitude up to 10 µV. Although the ERN can be observed after aware and unaware errors, the amplitude increases when the subject is instructed to pay attention to accuracy over speed (Falkenstein et al., 2000; Gehring et al, 1993; Olvet & Hajcak, 2008). The ERN derives from frontocentral areas, at the position of the FCz electrode, so the origin of the ERN is assumed to be within the ACC (Olvet & Hajcak, 2008; Gehring et al., 2018). Studies on the ERN show the relevance of error processing for various diseases. While anxiety and depression are associated with an increased ERN (Olvet und Hajcak, 2008), patients with substance abuse problems (Olvet und Hajcak, 2008) and borderline personality disorder (de Bruijn et al., 2006) show a decreased ERN. Based on the assumption that error processing is modulated by the mesencephalic dopamine system, studies analyzing the influence of medications that manipulate the dopamine system came to the conclusion that stimulating amphetamines lead to an increased ERN, while sedative benzodiazepines (in this case Lorazepam) lead to a decreased ERN compared to placebos (de Bruijn et al., 2006). Another, less extensive analyzed, event-related potential that can be recorded after committing an error is the error related positivity (Pe) that peaks between 200 and 500ms after committing an error and that is thought to arise from activity within the ACC (more rostral than the ERN; Herrmann et al., 2004) and parietal regions (Falkenstein, et al., 2000). Some authors suppose that in contrast to the ERN, the Pe is related to awareness of making an error (Herrmann et al., 2004), while others do not support this hypothis and assume that the Pe may eventually reflect a subjective/emotional process regulated by the individual importance of the error (Falkenstein et al., 2000). Some authors suppose that in contrast to the ERN, the Pe is related to awareness of making an error (Nieuwenhuis et al., 2001), while others do not support this hypothesis and assume that the Pe may eventually reflect a subjective/emotional process regulated by the individual importance of the error (Falkenstein et al., 2000).

Several functional imaging studies confirmed the involvement of the ACC in error processing. Hester and colleagues (2004) compared three functional magnetic resonance imaging (fMRI) studies using the go/no-go task and found congruent activity in the ACC, pre-

SMA, bilateral insula, thalamus, and right inferior parietal lobe (IPL). However, Neta and colleagues (2015) compared twelve experiments and found a much more extended network that showed differential activity between errors and correct trials distributed across cortical, subcortical, and cerebellar regions. They used a wide range of task types with different stimulus input (visual, auditory) and response output (button press, speech), what is a good assumption to generalize the results for error processing per se but then only a few experiments of each task type are included what reduces the power of the analysis.

In the literature there are two theories about the underlying neural mechanisms of error processing. The first one assumes a specific comparator system for error processing, that compares the intended response to the actual response (Ullsperger & von Cramon, 2001). The other one claims no specific system for detecting errors but a more general, unitary system for monitoring of cognitive conflict, including errors (Carter et al., 1998). Carter and van Veen (2007) described *conflict* as the presence of "competing, concurrently active, mutually incompatible representations". From this point of view errors can be seen as a special case of conflict in the way that the intended outcome and the actual outcome are incompatible. Incompatible representations are probed in several *interference tasks*. A good example of such a task is the Stroop task (Stroop, 1935), where in the classical version color words written in different ink colors are presented and the subject is asked to name the color of the ink and ignore the meaning of the word. In this example, the two representations are the ink color and the meaning of the word. An incompatible trial could for example be the word blue written in red, so the subject has to process these two different representations, but only react to the ink color and simultaneously inhibit the incongruent word meaning. When the word red written in red appears, no conflict arises, because both representations are mapped to the same response and do not compete against each other. *Conflict monitoring* describes the process to detect cognitive conflict. While the ACC is suggested to be responsible for this monitoring function, the DLPFC appears to be the top down instance to reduce conflict (MacDonald et al., 2000).

As already mentioned above some authors assume that the monitoring of errors is a part of conflict monitoring (Carter & van Veen, 2007). If this is the case the underlying neural correlates of error processing and cognitive conflict should be the same. This corresponds with the findings of some studies that even after correct trials an ERN can occur, even though the amplitude is smaller than after erroneous trials (Scheffers & Coles, 2000). However, other studies suggest that different parts of the cingulate cortex are associated with error processing versus conflict monitoring, with the rostral ACC being more involved in error processing and the caudal ACC in conflict monitoring (Garavan et al., 2003; Kiehl et al., 2000; Ullsperger & von Cramon, 2001).

The aim of this master´s thesis was to find out if there is a specific network for error processing and to compare this network to the neural structures involved in conflict monitoring via ALE meta-analyses. A lot of work has been done on fMRI-studies analyzing the neural correlates of error processing. All these studies have in common, that the reliability is low due to a rather small sample size. However, a meta-analysis looks for convergence of activity across studies and therefore is more reliable (Eickhoff et al., 2012). The weakness of prior summarizing work on error processing is that they had not enough studies for a quantitative meta-analysis, which should at least include seventeen experiments (Eickhoff et al., 2016). In this work all main analyses comply with this condition.

Errors can happen in various kind of tasks. In the present meta-analyses only studies using paradigms probing cognitive interference were included because most work on error processing and conflict monitoring focused on this tasks. A few authors analyzed the neural correlates of error processing for other tasks, e.g. for speech production and perception with a tongue twister task (Gauvin et al., 2016), for planning abilities in the Tower of London task (Unterrrainer, 2004) or for detection of emotions in prosody (Wittfoth, 2009), but there were not enough studies to perform separate analyses on these type of studies.

On the basis of prior work it can be expected that the ACC, pre-SMA and parietal areas as well as the bilateral insula and the thalamus are involved in error monitoring (Hester et al., 2004). Comparing error processing and conflict monitoring the hypothesis is that there will be more convergence across studies for error processing in the rostral part of the ACC, while conflict monitoring is supposed to be more caudal in the cingulate cortex. Additionally, stronger constant activity in the left lateral frontal cortex (Braver et al., 2001; Kiehl et al., 2000) is assumed for error processing compared to conflict monitoring. In contrast, stronger significant convergence across studies is assumed in the pre-SMA for conflict monitoring (Ullsperger and von Cramon, 2001).

Method

Search strategy and selection criteria

Different databases were used to obtain relevant experiments for the meta-analysis, namely PubMed (www.pubmed.org), Google Scholar (www.scholar.google.de), and Web of Science (www.webofknowledge.com). Search terms used were *error processing*, *error monitoring,* and *error checking*; always combined with the term *fMRI*, *neuroimaging* or *PET*. Additional studies were obtained from review articles and reference tracing from the retrieved papers.

The present meta-analyses include only neuroimaging studies covering the whole brain with reported activation foci as three-dimensional coordinates (x, y, z) in a standard reference space (Talairach & Tournoux, 1988) or Montreal Neurological (MNI; Collins et al., 1994). No studies using positron-emission tomography (PET) were found, therefore only data from fMRI were included. Studies reporting only results from region-of-interest (ROI) analyses were excluded. The reason to exclude results from ROI analyses in the activation likelihood estimation (ALE) approach is that convergence across experiments is tested against a null hypothesis that the individual foci are randomly distributed across the whole brain and each voxel has the a priori same chance of being activated (Eickhoff et al., 2012). However, ROI analysis test for effects only within a special area of the brain, which would violate the assumption of each voxel having a priori the same chance of being activated. For the same reason partial-brain-studies were excluded as well.

For generating a representative sample only data from healthy adults were included. All samples containing children or patients with any kind of physical or mental disease without reporting data from a healthy control group were excluded; as well as data from humans in altered physiological stage, like after deprivation of sleep, Transcranial Magnetic Stimulation, or medical manipulation. Also, studies manipulating the outcome (e.g. punishment after making an error) without reporting results for a control condition, were excluded.

Furthermore, only studies were included which calculated at least one of two contrasts: one was error trials showing more activity than correct trials (error > correct trials), the other was error trails showing higher activation compared to baseline activity (error > baseline activity). For the inverse contrasts (less activity for error trials compared to correct trials or baseline activity) there were not enough experiments to include them in the present study and perform separate analyses to look for convergent deactivations. Finally, only those studies that investigated error processing during paradigms probing cognitive interference were included. The reason behind this was that most studies investigating error processing use interference paradigms and in a further step a comparison to a previous meta-analysis investigating the neural correlates of successful interference control was performed. Moreover, it was taken care of not including multiple experiments from the same subject group to avoid driving convergence. Therefor studies using the same subject group as an already included study were excluded from the analyses.

After these criteria were applied 37 studies with 38 eligible contrasts remained (Tab.1). In case of one study including more than one experiment, those two contrasts that came from the same set of subjects were pooled into one experiment, to avoid that the analysis was driven by these studies. All included studies were published between 2000 and 2017. The sample size varied between seven and 102 participants. Most studies included male and female participants. Five studies only included male participants, while three studies gave no information on the sex of the subjects. Furthermore, three studies (Braver et al., 2001; Fassbender et al., 2004; Ullsperger and von Cramon, 2001) reported the sex of the participants included in the entire sample but excluded subsequently participants for the analysis and gave no information on the sex of the excluded participants. Thus, the sex of the remaining subjects of the sample used for the analysis is unknown. The participants were mostly righthanded and had a mean age between 22 and 40 years. One study reported no mean age, the range of age in this study was between 22 and 42 years (for details see Tab.2).

Seven authors were contacted per e-mail and asked for further information on the collected data (Allen et al., 2013; Edwards et al., 2012; Grützmann et al., 2016; Sagaspe et al., 2011; Simões-Franklin et al., 2010; Campanella et al., 2017; Ford et al., 2009) because they analyzed error processing but did not report the data needed for the present analysis with regard to the inclusion and exclusion criteria. Unfortunately, no response was received (so these studies could not be included in the meta-analyses).

Paradigms included

Neuroimaging results on the neural correlates of nine different tasks probing cognitive interference were included in the meta-analysis, namely the Flanker, Go/no-go, Stroop, Simon task, Antisaccade and Stop-signal tasks (SST), Sustained attention to response task (SART) and Multi-source interference task (MSIT). These paradigms are described below.

Flanker task.

In the Flanker task (Eriksen and Eriksen, 1974), participants are briefed to look at a fixation cross and afterwards identify and react (by pressing a button) to an upcoming target, like a letter or an arrow. Simultaneously, distractor stimuli (similar to the target) presented at both sides of the target stimulus have to be ignored. There are two different conditions of the task. For compatible trials the same reaction is associated with the target and the distractor stimuli, while in incompatible trials a different reaction is associated. For example, if the participant has to react to H and C with the left hand and to S and K with the right hand, an example for a congruent trial is HHCHH and an incongruent trial could be HHKHH. An error would be to push the wrong button (right vs. left). Usually incompatible trials produce more errors than compatible trials.

Go/no-go task.

In the Go/no-go task, participants are instructed to respond to an upcoming stimulus (e.g. the letter Y) and withhold the response to another stimulus (e.g. the letter X). The response usually is a button press with the index finger (cf., Kiehl et al., 2000). The common error that is made in this paradigm, namely to fail withholding the reaction to the stimulus that does not require a reaction, results from an increased response tendency due to higher frequency of go trials compared to no-go trials.

Stroop.

In the (standard) color-word Stroop task (Stroop, 1935), the participants are shown a list of (color-)words written in different colors. The challenge is to name the ink color of the word and inhibit reading the word. For congruent trials ink color and the word meaning are equal (e.g. the word blue printed in blue), while for incongruent trials ink color and word are different (e.g. the word yellow printed in red). Additionally, for neutral trials ink color and word do not provide competing responses (a color-word written in black ink). Incongruent trials produce slower reaction times and more errors are committed than for congruent trials (Tang et al., 2006).

Additionally to the color-word Stroop task, the numerical Stroop task was included in the meta-analysis. Here participants have to mention which of two presented numbers is physically larger (and not numerically). Congruent trials show two numbers that are larger in both modalities: physically and numerically. However, for incongruent trials the physically larger number is numerically smaller. For neutral trials the same numbers are presented in different sizes (Tang et al., 2006).

Simon task.

In the Simon task (Simon, 1990) participants have to react to an upcoming target with a right or left button-press. The color of the target determines the side, e.g., a blue target requires a left-hand response and a red target a right-hand response. Participants have to react to the color-response coding while concurrently ignoring the spatial placement of the target. For incongruent trials, where the target appears in the opposite hemifield of the color-coded reaction (e.g. a blue target presented in the right hemifield), participants have longer reaction times as for congruent trials (e.g. a blued target presented in the left hemifield). An error is committed when the participant pushes the wrong button (left vs. right).

Antisaccade task.

In the Antisaccade task (Hallett, 1978), the participants are instructed to fixate a central position and when a target appears, the have to look at the target (prosaccade) or in the opposite direction (Antisaccade), e.g. when the target appears on the left the participant has to look to the right. The common error here is, when participants in the Antisaccade condition look towards the target.

Stop-signal task (SST).

In the SST (Lappin and Eriksen, 1966; Logan et al., 1997), two different stimuli are presented. The two stimuli require different reactions (e.g. when an O appears participants have to make a left-hand button press, when an X appears participants have to make a right-hand button press). In trials where an additional auditory stimulus is presented participants have to inhibit the (already started) reaction. An error here is when participants fail to cancel to already initiated action.

Sustained attention to response task (SART).

The SART (Robertson et al., 1997) involves the withholding of a reaction to a rare target. For example, numbers from one to nine are presented in ascending (fixed SART) or random (random SART) order. The participants have to react to all numbers but the number three with a button press. When the number three appears, participants have to withhold the reaction. The common error here is to fail inhibiting the reaction to the rare stimulus.

Multi-Source Interference Task (MSIT).

The MSIT (Bush et al., 2003) is a combination of the Stroop, Flanker, and Simon task. In the MSIT participants are instructed to react to various numbers by button-presses with different fingers, e.g. to the number one with the index finger, to number two with the middle finger and to number three with the ring finger. Always three numbers are presented at the same time and the participant has to decide which of the numbers is different from the others (incongruent trials), e.g. for 221 the participant has to push the button with the ring finger, because the third number is different from the two other numbers. Additionally, the numbers are printed in different physical size (in the example the 1 can be printed smaller or bigger than the other number). In the control condition one number is presented with two X´s, e.g. 3XX or X1X.

Assignment of paradigms to sub-groups.

As mentioned above only studies using interference paradigms were included in the analyses. These paradigms were divided into two sub-groups, namely response inhibition and incongruence paradigms. Paradigms where the subject had to inhibit or cancel a motor response were assigned to *response inhibition paradigms*, namely the SST, Go/ no-go and SART. Those paradigms that required participants to inhibit a predominant motor response and initiate an incongruent response instead were assigned to *incongruence paradigms*, namely the Flanker task, MSIT, Stroop, Antisaccade task and the Simon task.

Activation Likelihood Estimation meta-analysis

Activation Likelihood Estimation (ALE) meta-analysis is one of the most commonly used algorithm for coordinate-based meta-analysis. The goal of ALE is to find out where the convergence of foci across experiments is higher as it would be expected if the results were randomly spatially distributed (Eickhoff et al., 2009). In this thesis the revised ALE algorithm for coordinate-based meta-analysis of neuroimaging results (Eickhoff et al., 2009, 2012; Turkeltaubet al., 2002) was used to identify convergent neuroimaging activation across experiments according to the standard procedures of the Forschungszentrum Jülich (Langner and Eickhoff, 2013; Rottschy et al., 2012).

Initially, for the meta-analysis coordinates reported in Talairach space were transformed into standard MNI space by linear transformation (Lancaster et al., 2007) and all given foci (x,y,z coordinates) are projected onto a brain template for display (Fig. 1.1). Afterwards a *modelled activation (MA) map* was computed for every experiment. This map contains for each voxel the probability of an activation being located at exactly that position considering spatial uncertainty. The results of single neuroimaging studies are limited by uncertainty in spatial location due to between-subject variance and between-template variance (Eickhoff et al., 2009). Between-subject variance arises from small sample size, while between-template variance results from different normalization strategies of various laboratories. To overcome this problem the ALE algorithm treats reported foci not as single points but as centers of three-dimensional Gaussian probability distributions. Assuming that studies with a larger sample size show less spatial uncertainty (they show more "true" and less random activation) the algorithm weights experiments with a larger sample size more by giving experiments with more subjects a smaller Gaussian distribution (Eickhoff et al., 2009). The resulting ALE map, which contains the MA maps of the included experiments, shows the local convergence across experiments (Fig. 1.2). In the last step, these results are compared to an empirical null distribution, to distinguish true convergence between experiments from random convergence, e.g. noise. This null distribution is based on the idea of random spatial association across the whole brain under the assumption that each voxel has the a priori same chance of being activated. This final resulting map shows the significant convergence across all included experiments (Fig. 1.3). Results are reported for a cluster level family-wise error (FWE; Eickhoff et al., 2012) corrected p value of <.05, with a cluster forming threshold of p < 0.001 on the voxel level. To label the resulting brain areas, the SPM Anatomy Toolbox 2.2c was applied (Eickhoff et al., 2005; http://www.fz-juelich.de/inm/inm1/DE/Forschung/_docs/SPMAnatomyToolbox/SPMAnatomyToolbox_node.html).

Analyses performed

A previous simulation work showed that each meta-analysis should at least include seventeen experiments to avoid that results are driven by individual experiments (Eickhoff et al., 2016). Therefore, only analyses were performed that fulfill this condition.

Three analyses were calculated: The main analysis of included all experiments of error processing during paradigms that probed cognitive interference. Separate subanalyses were performed on error processing during those experiments only that required participants to inhibit or cancel a motor response (response inhibition paradigms) and for those that required participants to inhibit a predominant motor response and initiate an incongruent response instead (incongruence paradigms). The analysis of error processing during response inhibition paradigms with a total of 20 experiments included the SART, the go/no-go and stop-signal task. Paradigms included in the analysis of error processing during incongruence paradigms with a total of 17 experiments were the Flanker, Stroop, Simon, Antisaccade tasks, as well as the MSIT. This separation was done to find out if there is a difference between error monitoring during paradigms were the motor response has to be inhibited without initiating an alternative response and those that require not only inhibition but also an alternative response to the inhibited one. Additionally, these three main analyses, i.e., error processing during (i) cognitive interference paradigms in general, (ii) response inhibition paradigms, and (iii) cognitive inhibition paradigms were repeated with only including the contrast error > correct trials.

As described above various authors suppose that error processing activates the same network in the brain as processing of cognitive conflict (e.g. Carter & van Veen, 2007). Therefore, here the idea was to compare both networks. Previous meta-analyses have already found neural correlates for the presence of cognitive conflict (Cieslik et al., 2015). With permission of the author these data were integrated to the data of experiments analyzing error processing and used to compare the neural correlates of error processing with those of cognitive conflict. In particular, a meta-analytic contrast with two directions was calculated: one for brain areas showing more convergence across experiments for error processing than for cognitive conflict (error > cognitive conflict) and one for those brain areas showing more convergence for cognitive conflict than for error processing (cognitive conflict > error). For the present analysis 150 experiments on processing of cognitive conflict in healthy adults were included (for comparison of demographic data of participants in the meta-analyses of error processing vs. cognitive conflict see Tab. 3). Sixteen experiments were excluded from the original study for better comparison because they used PET and the meta-analysis across error processing only included fMRI studies. The paradigms included in the experiments analyzing cognitive conflict were similar to the paradigms included in the meta-analysis for error processing (namely the Stroop, Flanker, Simon, SRC, Antisaccade, Go/no-go and SST). In a last step those voxels were identified where a significant effect was present in both separate analyses of error processing and conflict monitoring, conjunctions were computed using the conservative minimum statistic (Nichols et al., 2005; for steps of the meta-analyses see Fig. 7).

Results

Meta-analysis of error processing during interference tasks

In a first step, those brain regions were identified showing significantly convergent activity across all 38 experiments analyzing error processing during interference tasks, comprising 842subjects. For this main analysis six cluster revealed (Tab. 4a; Fig. 2.1), containing the ACC extending into the left SMG and the left pre-SMA, as well as the left and right aI extending into the right IFG and the bilateral supramarginal gyrus of the parietal lobe and the left DLPFC.

Sub-analysis of error processing during response inhibition paradigms

The meta-analysis across error processing during response inhibition paradigms included 20 experiments, comprising 474 subjects and revealed three cluster for significant convergence (Tab. 4b; Fig. 2.2), located in the ACC extending into the aMCC and adjacent left and right pre-SMA, as well as the bilateral aI extending into the bilateral IFG.

Sub-analysis of error processing during incongruence paradigms

The meta-analysis across error processing during incongruence paradigms included 17 experiments, comprising 346 subjects. Five cluster revealed showing consistent activity (Tab. 4c; Fig. 2.3), encompassing the ACC extending into the left SMG and the left pre-SMA, as well as the bilateral aI extending into the bilateral inferior frontal gyrus (IFG) and the left supramarginal gyrus.

Meta-analyses of error processing only including the contrast error > correct trials

Additionally, the main analysis of error processing during interference tasks and both reported sub-analyses of response inhibition paradigms and incongruence paradigms were repeated only including the contrast error > correct trials. Experiments only including the contrast error > baseline were excluded for this analysis. The reason behind this was to have a direct comparison of task-specific activity for error and correct trials because both conditions include a motor response, while baseline activity does not. Therefore, these analyses should only reveal brain regions specifically for error processing, without those appropriate for processing of the motor response. Importantly to mention, these analyses were done complementary to the prior analyses for a first impression but are not representative because they included less than the previously mentioned obligatory 17 experiments necessary for an informative analysis.

After excluding experiments only using the contrast error > baseline activity almost the same brain regions showed consistent convergence as for the analysis including both contrasts. For the main analysis of error processing during interference tasks the analysis only including the contrast error>correct trials revealed five cluster, including all cluster of the main analysis including both contrasts. The only exception was, that no consistent convergence was found in the right supramarginal gyrus. For error processing during incongruence paradigms there was convergence across studies for the same brain regions as in the analysis including both contrasts. For error processing during response inhibition paradigms the left insula showed no convergence, the other brain areas were the same as in the prior analysis pooling across error>correct and error>baseline.

Meta-analysis of conflict resolution during interference tasks

This analysis was done to reveal those brain regions showing significant convergence of activity for conflict resolution during interference tasks. Therefore, 148 experiments, comprising 2320 subjects, were included. Eight cluster revealed showing significant convergence (Tab. 4d, Fig. 2.4), comprising the bilateral aI extending into the left pre-SMA, the right SFG, the right IFG and adjacent the right aMCC and the right MFG. Moreover, convergent activity was found in the bilateral intraparietal sulcus (IPS) extending into the left superior parietal lobe (SPL), the left angular gyrus, as well as the right supramarginal gyrus and the right superior temporal gyrus (STG), the left precentral gyrus and the left IFG, as well as the left dorsal premotor cortex. Additionally, consistent activity was located in the left inferior occipital gyrus (IOG) extending into left middle occipital gyrus (MOG), the right thalamus and the right caudate nucleus.

Contrast of error processing vs. conflict monitoring

In a next step, a contrast analysis was performed comparing convergence across studies during error processing with those during conflict resolution. Eight cluster revealed stronger convergence during error processing, comprising the ACC extending into the pre-SMA, as well as the bilateral aI extending into the bilateral IFG, the bilateral supramarginal gyrus and the left MFG (Tab.4e; Fig. 3).

In contrast, nine cluster revealed stronger convergence during conflict monitoring, encompassing the bilateral IFG extending into the bilateral MFG, as well as the bilateral SPL extending into the left IPS, the left IPL and the left postcentral gyrus. Moreover, stronger convergence for conflict monitoring was found in the bilateral superior frontal gyrus (SFG), the left IOG extending into the left fusiform gyrus, as well as the right caudate nucleus and the aMCC (Tab. 4f; Fig. 3).

The conjunction across both analyses revealed conjoint activity of the SMG extending into the pre-SMA and the aMCC, as well as the bilateral aI and the right supramarginal gyrus (Tab. 4g; Fig. 4).

Discussion

Summary

In this master´s thesis the neural correlates of error processing during interference tasks were calculated via ALE meta-analysis. A total of six brain regions showed significant convergence across studies for the main analysis of error processing, namely the ACC extending into the pre-SMA, the bilateral aI and the bilateral supramarginal gyrus in the parietal cortex, as well as the left DLPFC. The two sub-analyses of error processing during response inhibition paradigms and incongruence paradigms both showed consistent convergence for the ACC extending into the pre-SMA and the bilateral aI, but only for incongruence paradigms also the cluster in the left DLFPC and the left supramarginal gyrus were consistently involved. The same brain regions showed constant convergence for the additionally performed analyses including only the contrast of error>correct trials with the exception that the right supramarginal gyrus was not consistently found for the main analysis of error monitoring and the left insula not consistently for error monitoring during response inhibition paradigms.

In a next step, the brain regions of the main analysis for error processing were compared to the network consistently found during conflict monitoring. Various brain regions showed more convergence for conflict monitoring, namely the bilateral IFG, the bilateral MFG, the bilateral SPL, the left IPS, the left IPL and the left postcentral gyrus, as well as the bilateral SFG, the left IOG, the left fusiform gyrus, the right caudate nucleus and the pre-SMA. However, for error processing the ACC extending into the pre-SMA, the bilateral aI, the bilateral supramarginal gyrus and the left MFG showed stronger convergence. The conjunction across error processing and conflict monitoring revealed conjoint activity of the SMG extending into the pre-SMA and the aMCC, as well as the bilateral aI and the right supramarginal gyrus.

The present meta-analyses show the robust involvement of the ACC, the pre-SMA and the bilateral aI for error processing during interference tasks, even if separately performed for response inhibition and incongruence paradigms. The ACC is assumed to have a monitoring function for errors, or more general for cognitive conflict (van Veen and Carter, 2002). In line with prior work the rostral part of the ACC showed stronger convergence for error processing than for conflict monitoring, supporting the hypothesis that the more anterior part of the cingulum is specifically involved in control processes after committing an error. While prior literature focused on the ACC, these analyses revealed also consistent activity in the aMCC for error processing, as well as conflict monitoring. This region has been related to feedback-related activity (Amiez et al., 2013). Thus, it can be assumed that the aMCC monitors the response after a trial. Ullsperger and von Cramon (2001) proposed the pre-SMA being rather involved in conflict monitoring than in error processing. The results of these analyses can not support this assumption. In contrast, the pre-SMA showed stronger involvement during error processing, while the conjunction analysis revealed also conjoint congruent activity for this region. It seems more plausible that the pre-SMA is involved in monitoring of both error commission and cognitive conflict (Fassbender et al., 2004). Surprisingly, there was also stronger convergence for error processing in the bilateral aI. Prior work on the aI claims this region to be involved in goal-directed behavior and focal attention (Nelson et al., 2010). This can explain the stronger involvement of the aI in error processing over conflict monitoring in the way that errors heighten the attention to the task to avoid committing errors in the future. In contrast to prior work no convergence was found for the thalamus (Hester et al., 2004). Due to that fact that Hester and colleges (2004) only included experiments were the subjects had to perform the Go/no-go task it can be argued that activity in the thalamus may be task specific and can not be generalized to error processing during interference tasks per se.

An interesting finding is that the left DLPFC and the bilateral supramarginal gyrus were consistently involved in error processing only for the incongruence paradigms. According to the theory of the DLPFC being the top-down instance to reduce conflict (MacDonald et al., 2000) it should be generally involved during error processing for both, response inhibition and incongruence paradigms. However, Fiehler and colleagues (2004) assumed that error-related activation in the lateral prefrontal cortex (LPFC) was more related to Go/no-go tasks (response inhibition paradigm) than Flanker tasks (incongruence paradigm). In contrast, the present analyses only revealed congruent activity in the left DLPFC for incongruence paradigms. One could argue that incongruence paradigms are more complex because here participants not only have to inhibit the congruent response but concurrently perform an incongruent response and therefore more top-down control is needed. The finding of significant convergence only for the left DLPFC during error processing confirms the work of Garavan and colleagues (2002) who assumed the right DLPFC being involved in successful response inhibition and the left DLPFC being involved in error processing or rather adjusting of errors. Thus, it seems that the left and right DLPFC reflect different processes during interference tasks. While the right DLPFC is related to inhibition of the motor response, the left DLPFC is involved in control processes after committing an error.

The other region showing convergence for the main analysis of error processing during interference tasks and for incongruence paradigms, but not for response inhibition paradigms was the supramarginal gyrus. Prior work on incongruence paradigms found a relation between parietal regions and awareness of committing errors. Hester and colleagues (2005) found more activity in parietal areas for aware than for unaware errors. This confirms with the theory of the Pe that can be deviated from parietal regions of the brain being related to awareness of committing errors (Nieuwenhuis et al., 2001) and an fMRI study that found more activity in the bilateral IPL for aware compared to unaware errors (Hester et al., 2005). However, other work only found more activity for aware compared to unaware errors in the anterior inferior insula (Klein et al., 2007). A second assumption is that the IPL is part of a network reflecting the recruitment of general attentional resources, to prevent future error commission (Rubia et al., 2003). Both of these theories can not explain why there was no significant convergence found in the supramarginal gyrus for errors during response inhibition paradigms. Further work is necessary to disentangle the function of the supramarginal gyrus during interference tasks.

Taken together these analyses revealed various regions being involved in error processing. As the conjunction analysis showed, most of these regions were also involved in conflict monitoring. But there were also areas showing constant activity especially after error commission, namely the rostral part of the ACC (Fig. 5), the lateral part of the bilateral aI and the inferior part of the right supramarginal gyrus, as well as the left supramarginal gyrus.

Thus, it seems that these regions are involved in control processes after committing of errors. Regarding to the question if there is a specific comparator system for error processing, these results rather argue for a more general, unitary system for monitoring of cognitive conflict, with errors being a part of it.

Conceptual considerations and directions for further research

The big advantage of meta-analyses is the high statistical power. To reach this power a sufficient quantity of already existing experiments is necessary. This leads to one limitation of the present meta-analytic approach. It would have been interesting to distinguish between errors of commission and errors of omission. However, most work focused on commission errors and there were not enough studies focusing on omission of errors to perform separate sub-analyses. Additionally, it was not possible to compare brain regions involved in processing of aware errors compared to unaware errors. This leaves the question open if the supramarginal gyrus may be involved in aware error processing. Future work should also focus on the function of parietal areas, specifically the supramarginal gyrus, during processing of errors. Furthermore, a lot of studies on error related activity and the presence of cognitive conflict focused on the ACC, while the present analyses also show the involvement of another part of the cingulum in both processes, namely the aMCC. The function of this region during error processing and conflict monitoring seems rather unclear and should be analyzed in subsequent studies. Moreover, the results of this work can only be related to interference tasks. Future work should try to find out if the results for interference tasks can be transferred to error processing in general.

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Tables

Table 1

Studies included in the meta-analysis

Publication	Subjects	Space	Paradigm	Contrast
Agam et al., 2011	30	TAL	Antisaccade	errror > correct trials
Barke et al., 2017	8	MNI	Flanker task	errror > correct trials
Braver et al., 2001	14	TAL	Go/ no-go	errror > correct trials
Carp et al., 2010	21	MNI	MSIT	error > correct trials
Chevrier et al., 2007	14	TAL	SST	error > baseline
Critchley et al., 2005	15	MNI	Stroop	error > correct trials
Debener et al., 2005	13	TAL	Flanker task	errror > correct trials
Fassbender et al., 2004	18	TAL	SART	error > baseline
Fiehler et al., 2004	27	TAL	Flanker task	errror > correct trials
Fitzgerald et al, 2005	7	MNI	Flanker task	errror > correct trials
Ford et al., 2005	10	TAL	Antisaccade	error > correct trials
Garavan et al., 2002	14	TAL	Go/ no-go	error > correct trials
Garavan et al., 2003	16	TAL	Go/ no-go	error > correct trials
Ham et al., 2013	35	MNI	Simon task	errror > correct trials
Hester et al., 2004	15	TAL	Go/ no-go	error > baseline
Hughes et al., 2012	10	MNI	SST	error > baseline
Iannccone et al., 2015	15	MNI	Flanker task	errror > correct trials
Kaufmann et al., 2003	14	TAL	Go/ no-go	errror > correct trials
Kerns et al., 2005	13	TAL	Stroop	errror > correct trials
Kiehl et al., 2000	14	TAL	Go/ no-go	error > correct trials error >baseline
King et al., 2010	21	TAL	Simon task	error > correct trials
Klein et al., 2007	13	TAL	Antisaccade	errror > correct trials
Ko et al., 2014	23	MNI	Go/ no-go	errror > correct trials
Li et al., 2008	40	MNI	SST	errror > correct trials
Lütcke and Frahm, 2007	11	MNI	Go/ no-go	errror > correct trials
Marco-Pallarés et al., 2008	10	MNI	Flanker task	error > correct trials
Matthews et al., 2005	16	TAL	SST	error > correct trials
Menon et al., 2001	14	MNI	Go/ no-go	error > correct trials

Table 1 (continued)

Publication	Subjects	Space	Paradigm	Contrast
Ramautar et al., 2006	16	TAL	SST	errror > correct trials
Rubia et al., 2003	20	TAL	SST	error > correct trials
Sharp et al., 2009	26	MNI	SST	errror > correct trials
Sosic-Vasic et al., 2012	27	MNI	Go/ no-go	errror > correct trials
Sozda et al., 2011	11	TAL	Stroop	errror > correct trials
Steele et al., 2014	102	MNI	Go/ no-go	errror > correct trials
Ullsperger and von Cramon, 2001	9	TAL	Flanker task	errror > correct trials
Wessel et al., 2012	21	MNI	Flanker task	error > baseline

Table 2

Information on participants of included studies

Publication	Subjects	Mean age	Gender (m vs f)	Handedness
Agam et al., 2011	30	36	20 vs 10	missing
Barke et al., 2017	75	22,2	14 vs 61	right-handed
Braver et al., 2001	8	22,9	missing	right-handed
Carp et al., 2010	21	39,8	15 vs 6	missing
Chevrier et al., 2007	14	29,4	8 vs 6	right-handed
Critchley et al., 2005	15	23	missing	right-handed
Debener et al., 2005	13	25,2	5 vs 8	right-handed
Fassbender et al., 2004	18	26,4	missing	right-handed
Fiehler et al., 2004	27	25	16 vs 11	right-handed
Fitzgerald et al, 2005	7	30	5 vs 2	missing
Ford et al., 2005	10	28	7 vs 3	right-handed
Garavan et al., 2002	14	30	4 vs 10	right-handed
Garavan et al., 2003	16	31	6 vs 10	right-handed
Ham et al., 2013	35	30,6	17 vs 18	missing
Hester et al., 2004	15	30	5 vs 10	right-handed
Hughes et al., 2012	10	35.1	7 vs 3	right-handed
Iannccone et al., 2015	15	25,4	missing	right-handed
Kerns et al., 2005	13	36	9 vs 4	right-handed
Kiehl et al., 2000	14	28,4	7 vs 7	missing
King et al., 2010	21	27,9	21 vs 0	right-handed
Klein et al., 2007	13	26,15	5 vs 8	right-handed
Ko et al., 2014	23	24,35	23 vs 0	right-handed
Li et al., 2008	40	missing	20 vs 20	right-handed
Lütcke and Frahm, 2007	11	27	3 vs 8	right-handed
Marco-Pallarés et al., 2008	10	23	2 vs 8	right-handed
Matthews et al., 2005	16	34	9 vs 7	missing
Menon et al., 2001	14	23,6	8 vs 6	right-handed
Orr et al., 2012	56	27	49 vs 7	right-handed
Ramautar et al., 2006	16	26,25	8 vs 8	missing
Rubia et al., 2003	20	28	20 vs 0	right-handed

Table 2 (continued)

Publication	Subjects	Mean age	Gender (m vs f)	Handedness
Sozda et al., 2011	11	25,1	missing	missing
Steele et al., 2014	102	33,92	49 vs 53	7% left-handed
Ullsperger and von Cramon, 2001	9	24,9	missing	right-handed
Wessel et al., 2012	21	24,7	9 vs 12	one left-handed

Note. Missing data in the original studies are labeled as *missing*.

Table 3

Subjects included in analysis for error processing vs. subject included in analysis for cognitive conflict

Sex		Mean age (in years)		Handedness	
Error	Conflict	Error	Conflict	Error	Conflict
male and female	male and female	between 22 and 40	between 20 and 42	mostly righthanded	mostly righthanded

Table 4a

Brain regions of significant convergence of activity related to error processing during interference tasks

Macroanatomical Structure	x	y	z	z-score	Histological assignment
Cluster 1 (1568 voxels)					
Right ACC	2	30	24	7,27	
Left SMG	2	24	40	6,26	
Left preSMA	2	16	48	6,22	
	-2	16	60	4,98	
Cluster 2 (851 voxels)					
Right aI	44	16	-2	7,40	
	36	18	-14	5,16	
	34	26	0	3,58	
Right IFG	52	24	6	4,06	Area 45
Cluster 3 (771 voxels)					
Left aI	-38	20	-8	7,61	
	-44	4	4	3,67	
	-34	12	-18	4,09	
Cluster 4 (169 voxels)					
Left supramarginal gyrus	-60	-46	34	6,04	Area PFm (IPL)
Cluster 5 (151voxels)					
Right supramarginal gyrus	62	-42	30	4,74	Area PF (IPL)
Cluster 6 (97 voxels)					
Left DLPFC	-24	46	28	4,45	
	-30	52	28	4,41	

Table 4b

Brain regions of significant convergence of activity related to error processing during response inhibition paradigms

Macroanatomical Structure	x	y	z	z-score	Histological assignment
Cluster 1 (684 voxels)					
Right ACC	2	32	24	6,26	
	2	24	26	6,02	
Left pre-SMA	-4	16	44	4,63	
Right pre-SMA	4	18	48	4,30	
Left aMCC	-6	22	36	3,98	
Cluster 2 (236 voxels)					
Right aI	42	16	0	5,62	
Right IFG	48	20	-6	4,47	
Cluster 3 (163 voxels)					
Left aI	-36	16	0	4,03	
Left IFG	-38	20	-10	4,74	

Table 4c

Brain regions of significant convergence of activity related to error processing during incongruence paradigms

Macroanatomical Structure	x	y	z	z-score	Histological assignment
Cluster 1 (883 voxels)					
Left SMG	2	24	40	6,63	
Left pre-SMA	0	14	50	5,17	
	-2	16	58	4,14	
	6	12	64	3,31	
Left ACC	0	28	24	4,78	
Cluster 2 (570 voxels)					
Right aI	44	14	-4	6,25	
	40	24	-6	4,82	
	34	18	-12	3,61	
Right IFG	48	26	0	3,89	
	54	14	2	3,24	Area 44
	32	18	0	3,87	
Cluster 3 (531 voxels)					
Left aI	-36	22	-6	6,24	
Left IFG	-34	14	-18	3,61	
Cluster 4 (96 voxels)					
Left MFG	-24	-44	26	4,46	
	-30	50	26	4,13	
Cluster 5 (91 voxels)					
Left supramarginal gyrus	-60	-46	34	5,21	Area PFm (IPL)

Table 4d

Brain regions of significant convergence of activity related to conflict monitoring

Macroanatomical Structure	x	y	z	z-score	Histological assignment
Cluster 1 (5595 voxels)					
Right aI	36	22	-4	8,34	
Left pre-SMA	2	16	48	8,32	
Right IFG	50	14	28	8,29	
	48	12	30	8,08	
	48	30	24	6,35	
Right aMCC	8	28	34	6,60	
Right MFG	46	32	22	6,27	
	38	0	54	6,09	
	44	36	18	6,03	
Right SFG	26	0	60	4,72	
Cluster 2 (1449 voxels)					
Left IPS	-42	-42	46	6,87	Area hIP3 (IPS)
	-38	-44	46	6,79	Area hIP1 (IPS)
	-28	-62	40	5,89	Area hIP3 (IPS)
	-34	-56	42	5,02	Area hIP3 (IPS)
Left SPL	-24	-66	48	6,66	
	-14	-62	60	4,19	Area 7a (SPL)
Left angular gyrus	-40	-62	48	3,67	Area PGa (IPL)
Cluster 3 (1361 voxels)					
Right IPS	40	-46	46	7,18	Area hIP3 (IPS)
Right supramarginal gyrus	60	-44	24	5,41	Area PFm (IPL)
Right IPS	50	-36	42	4,34	Area hIP2 (IPS)
Right STG	52	-46	14	4,51	
Cluster 4 (785 voxels)					
Left precentral gyrus	-44	10	30	7,72	
Left IFG	-46	22	28	5,37	
Cluster 5 (772 voxels)					
Left aI	-34	20	-2	8,30	
Cluster 6 (449 voxels)					
Left dorsal premotor cortex	-26	0	54	6,3	

Table 4d (continued)

Macroanatomical Structure	x	y	z	z-score	Histological assignment
Cluster 7 (371 voxels)					
Left IOG	-40	-66	-10	5,58	Area FG2
	-36	-64	-20	4,48	Area FG2
Left MOG	-42	-78	4	3,55	Area hOc41a
	-44	-70	0	3,53	Area hOc5
Cluster 8 (362 voxels)					
Right thalamus	14	-6	10	5,73	Thal: Prefrontal
	6	-18	-4	4,66	Thal: Prefrontal
Right caudate nucleus	14	6	8	4,62	

Table 4e

Brain regions showing stronger convergence of activity related to error processing than to conflict monitoring

Macroanatomical Structure	x	y	z	z-score	Histological assignment
Cluster 1 (764 voxels)					
Right ACC	2	30	24	7,27	
Left preSMA	2	8	48	1,86	
Cluster 2 (420 voxels)					
Left IFG	-40	22	-8	7,27	
Left aI	-42	2	4	2,98	
	-42	-2	2	2,87	
	-42	8	4	2,81	
	-32	14	-18	2,80	
	-32	10	-18	2,78	
	-40	16	4	2,27	
Cluster 3 (262 voxels)					
Right aI	46	12	-2	3,67	Area 44
Right IFG	50	26	-10	3,26	
Cluster 4 (138 voxels)					
Left pre-SMA	-2	18	62	3,30	
Cluster 5 (137voxels)					
Left supramarginal gyrus	-62	-44	36	3,22	Area PF (IPL)
Cluster 6 (83 voxels)					
Left MFG	-24	44	26	2,88	
	-24	48	28	2,82	
	-28	52	32	2,30	
Cluster 7 (69 voxels)					
Right aI	32	18	-16	3,30	
	36	12	-18	3,22	
Cluster 8 (51 voxels)					
Right supramarginal gyrus	62	-44	36	2,25	Pfm (IPL)
	52	-40	30	2,19	

Table 4f

Brain regions showing stronger convergence of activity related to conflict monitoring than to error processing

Macroanatomical Structure	x	y	z	z-score	Histological assignment
Cluster 1 (628 voxels)					
Right IFG	42	6	24	3,30	
	38	20	14	2,70	
	56	16	16	2,31	Area 45
	36	32	28	2,18	
	46	34	12	2,03	Area 45
	42	30	14	2,00	
	44	14	18	3,28	
Right MFG	44	50	18	2,79	
	40	28	22	2,57	
	34	38	30	2,33	
	36	38	34	2,26	
Cluster 2 (571 voxels)					
Left SPL	-22	-70	46	5,25	
	-22	-66	44	5,09	
	-22	-72	50	3,94	
Left IPS	-24	-62	38	4,28	Area hIP3 (IPS)
Left IPL	-32	-40	44	2,62	
Left IPS	-30	-48	40	1,80	Area hIP1 (IPS)
Left postcentral gyrus	-44	-38	56	2,19	Area 2
Cluster 3 (424 voxels)					
Right SPL	32	-46	44	3,67	
	28	-50	44	3,49	
	28	-66	54	3,60	Area 7A
	26	-66	50	3,57	
Right IPS	28	-58	56	3,19	Area hIP3 (IPS)
Cluster 4 (343 voxels)					
Right MFG	40	4	58	3,09	
Right SFG	32	2	62	3,01	
	28	-2	66	2,57	
	36	0	44	2,31	
Cluster 5 (298 voxels)					
Left SFG	-22	-6	56	3,78	
Left MFG	-26	-2	48	3,54	

Table 4f (continued)

Macroanatomical Structure	x	y	z	z-score	Histological assignment
Cluster 6 (259 voxels)					
Left IOG	-36	-66	-8	3,67	
Left MOG	-44	-68	-2	2,98	
Left fusiform gyrus	-38	-58	-10	2,85	
	-32	-62	-16	2,57	Area FG1
Cluster 7 (246 voxels)					
Left IFG	-40	14	22	3,3	
Left precentral gyrus	-36	6	30	2,4	
Cluster 8 (156 voxels)					
Right caudate nucleus	12	6	10	3,67	
Cluster 9 (26 voxels)					
Right aMCC	14	6	56	2,05	
	14	10	54	2,03	

Table 4g

Brain regions of conjoint significant convergence of activity related to error processing and conflict monitoring during interference tasks

Macroanatomical Structure	x	y	z	z-score	Histological assignment
Cluster 1 (850 voxels)					
Left SMG	2	24	40	6,26	
Left preSMA	2	16	48	6,22	
	4	12	62	3,78	
Right aMCC	6	30	30	5,29	
Cluster 2 (673 voxels)					
Right aI	42	16	-4	6,73	
	36	20	-12	4,67	
	34	26	0	3,58	
Right IFG	52	22	4	3,89	Area 45
Cluster 3 (492 voxels)					
Left aI	-38	20	-6	6,78	
Cluster 4 (102 voxels)					
Right supramarginal gyrus	62	-42	30	4,66	Area PF (IPL)

Figures

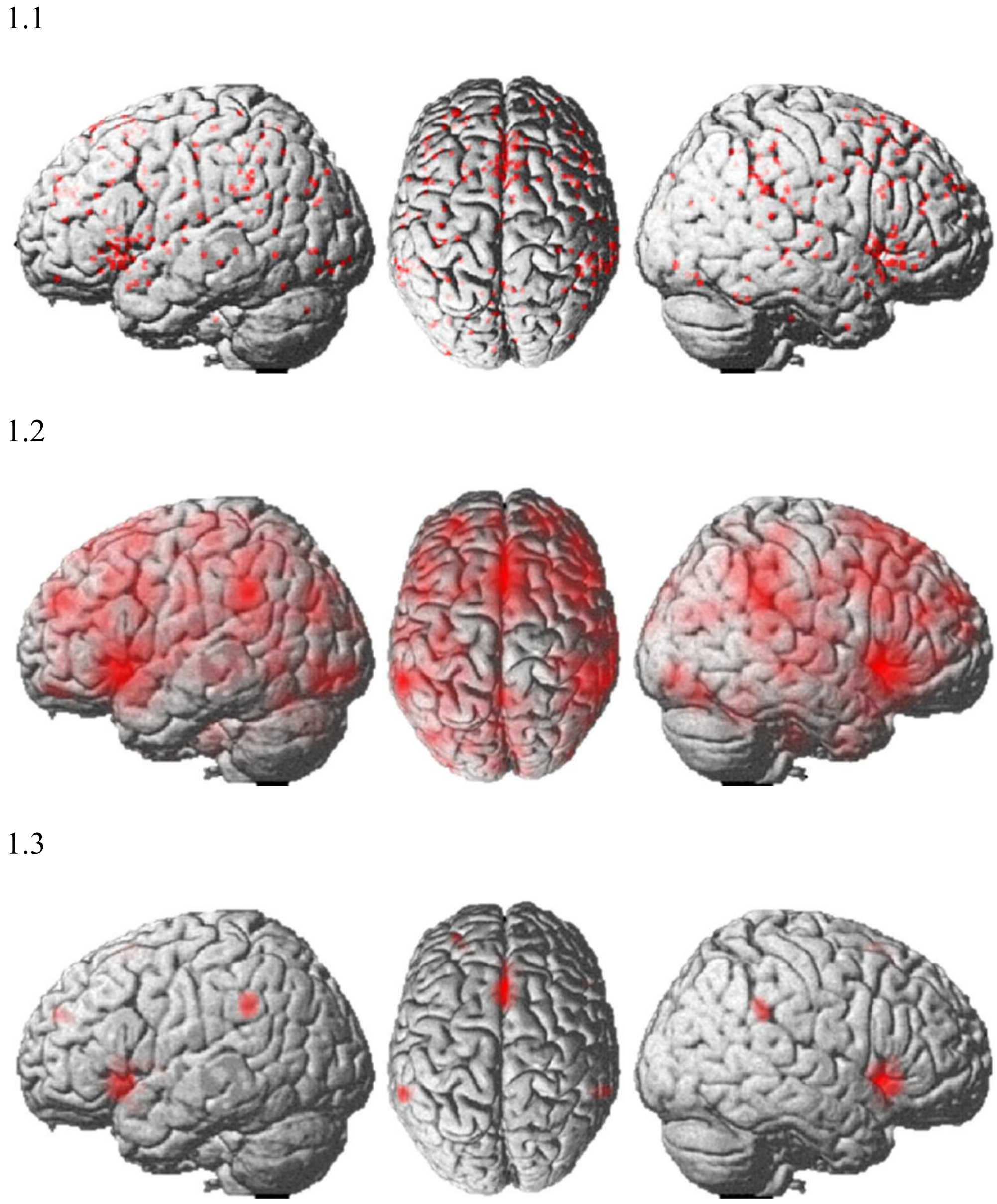

Figure 1. Steps of the ALE meta anaysis. 1.1 Given foci of included experiments in standard MNI space. 1.2 ALE map showing local convergence across experiments. 1.3 ALE map showing significant convergence across experiments

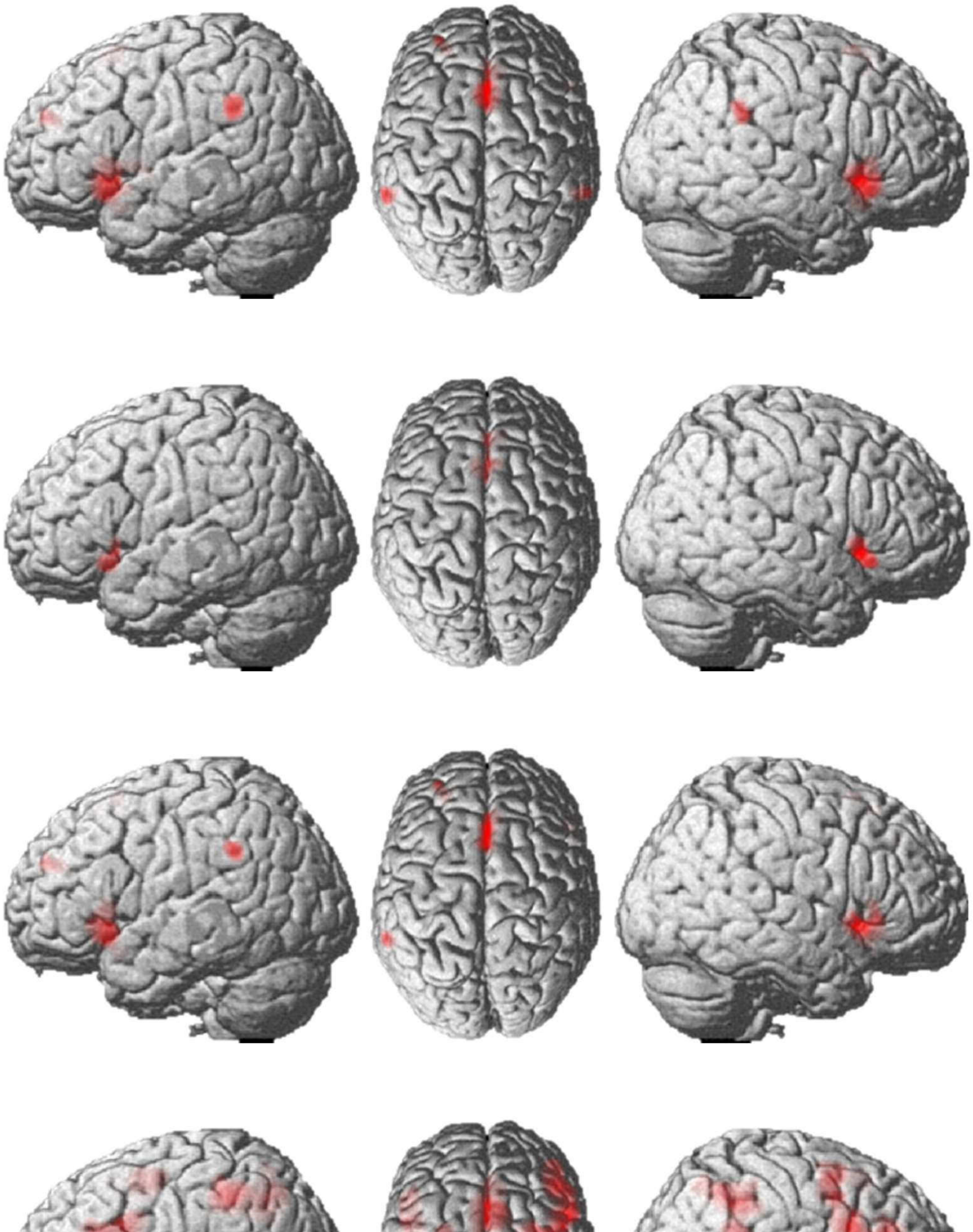

Figure 2. Cluster of brain regions showing significant constant activity across studies probing cognitive interference illustrated in red color. 2.1 for error processing 2.2 for error processing during response inhibition paradigms 2.3 for error processing during incongruence paradigms 2.4 for conflict resolution

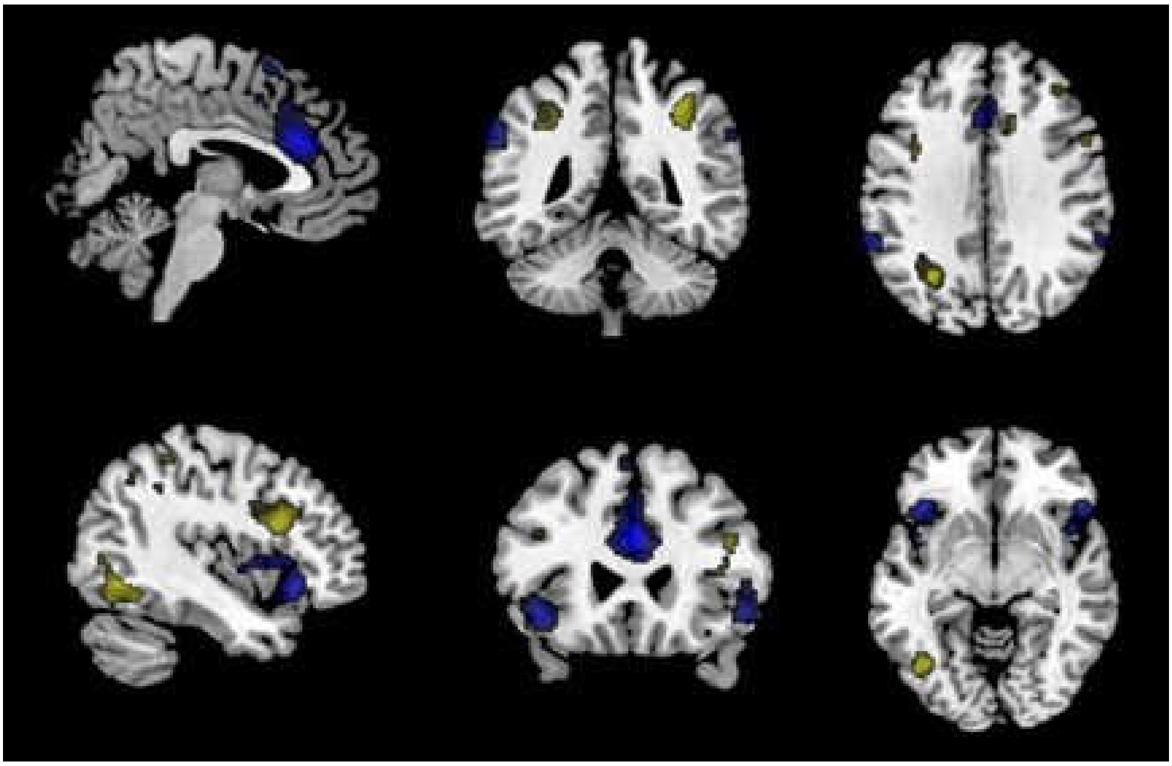

Figure 3. Sagittal slices (left) coronal slices (middle) and axial slices (right) showing the contrast of error processing vs. conflict resolution with stronger constant activity for error processing illustrated in blue and stronger constant activity for conflict resolution in yellow.

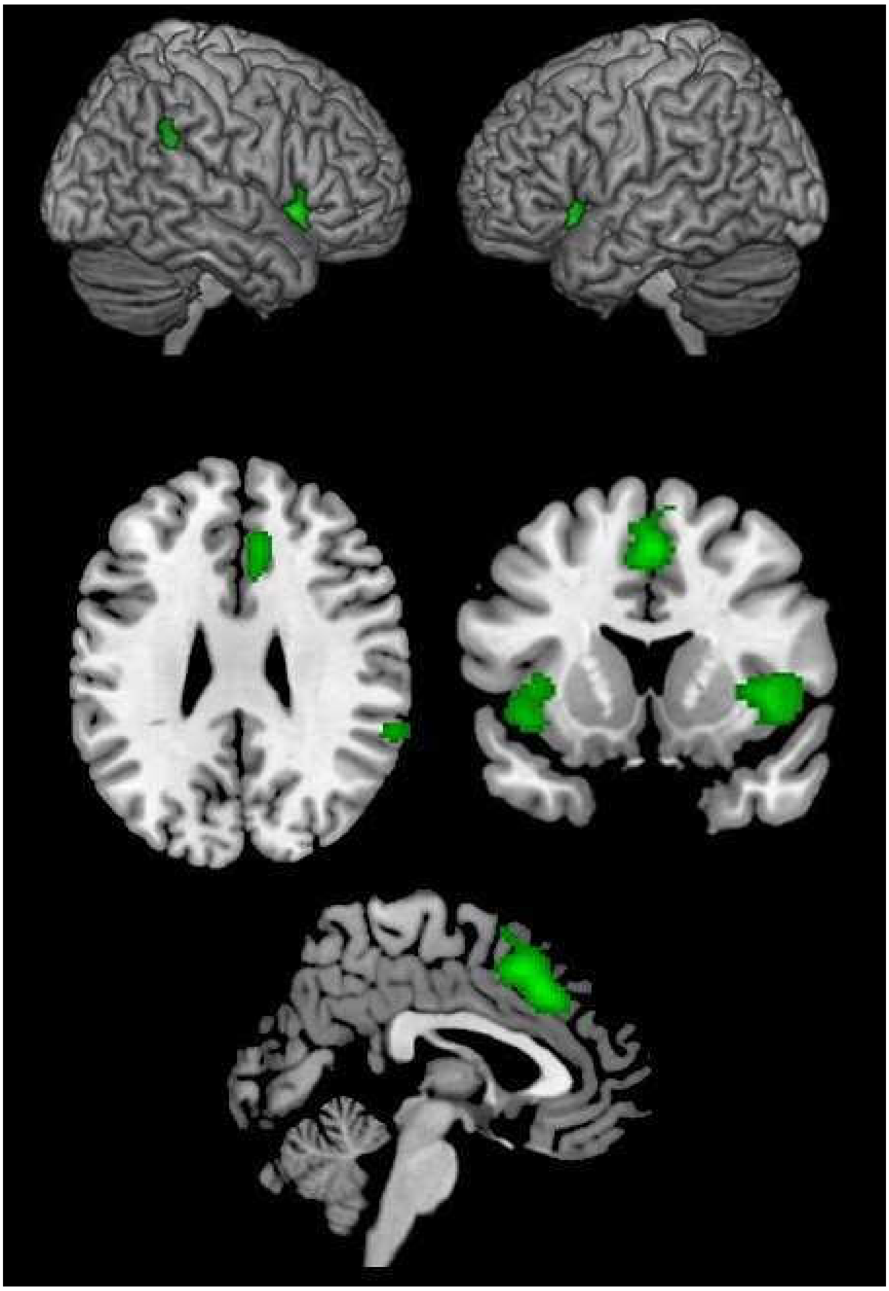

Figure 4. Cluster of conjunction analysis revealing conjoint consistent activity for error processing and conflict resolution illustrated in green.

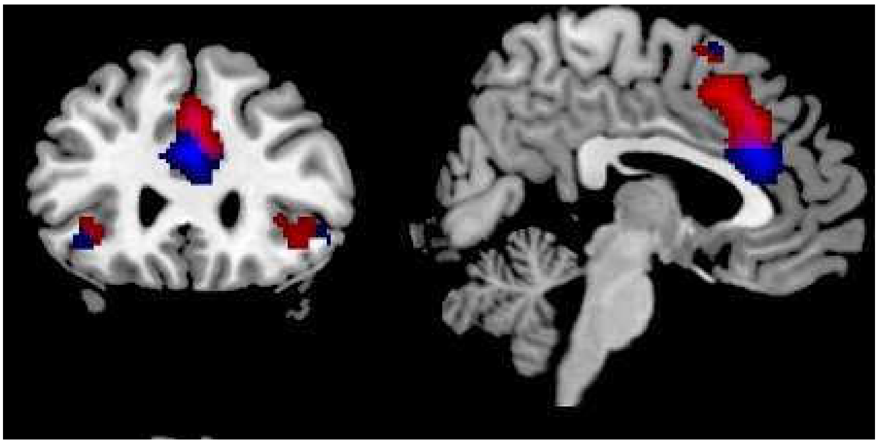

Figure 5. Conjoint consistent activity of error processing and conflict resolution illustrated in red compared to stronger consistent activity for error processing illustrated in blue.

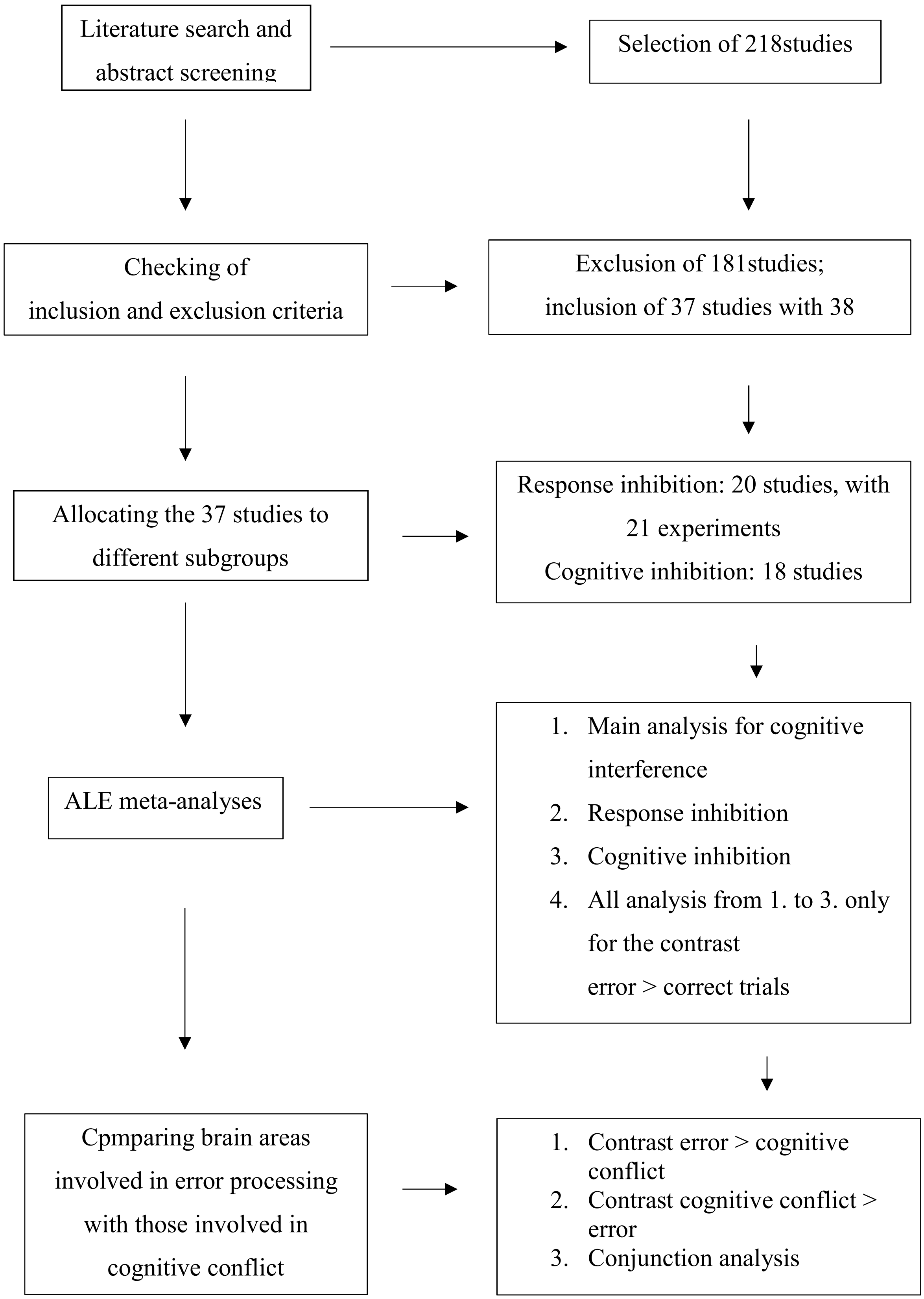

Figure 6. Steps of the meta-analyses