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Error processing beyond the response level

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CONTENTS

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CHAPTER 1

INTRODUCTION[1]

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INTRODUCTION

Errors are key features of human functioning, or as Seneca the Younger phrased it in *Ancient Rome,* "*Errare humanum est* (to err is human)." Typically, errors have a negative connotation, likely due to their potentially severe consequences (imagine car accidents, plane crashes, or even nuclear disasters). Yet errors play a vital role in our daily lives by signaling that a given behaviour is no longer appropriate, or that adjustments are needed; again, citing Seneca the Younger, "*Errare humanum est, perseverare diabolicum* (to err is human but to persist diabolical)." In recent decades, innumerable studies on error monitoring have emerged (for reviews see Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004; Ullsperger & von Cramon, 2004). Based on the above, this is not surprising. Examining error instances can illuminate how we achieve constant updating of our behaviour in a rapidly changing environment. Further, by studying errors we may determine the boundaries of human functioning, thereby preventing human disasters.

In the laboratory, a range of stimulus-response compatibility (SRC) tasks such as the flanker task (Eriksen & Eriksen, 1974) or the Simon task (Simon, 1969) have been frequently used to study errors. Typically in such tasks, a conflict at the response level occurs. In other words, participants have to execute a response while irrelevant information interferes with this correct response. For example, in the flanker task the direction of a central arrow has to be determined (left or right). Conflict occurs when the surrounding arrows, which should be ignored by the participant, point in the opposite direction and consequently activate the wrong response. During such instances of response conflict, response errors arise more frequently than in non-conflicting situations (i.e., situations in which all arrows point in the same direction). Thus, response errors and response conflict are typically studied within the same experiments.

The aim of the current dissertation is to broaden the point of view from which errors and conflict are studied. I will do this in three ways: First, we will extend the level from which errors and conflict are studied; rather than focusing solely on the response level, we will also study errors and conflict at the task level. Secondly, we will examine whether the error- and conflict-related effects usually described in laboratory tasks might be replicated when using more complex tasks, such as those encountered in daily life. Finally, we will investigate whether we use our internal error-monitoring network for understanding errors we did not commit ourselves, but merely observed. In particular, we will examine whether the same brain regions are involved when observing human errors and machine errors. Below, I will broadly outline previous research conducted on error processing. Thereafter, I will discuss the three research lines in more detail.

ERROR PROCESSING: CURRENT STATE OF AFFAIRS

BEHAVIOURAL CORRELATES OF ERROR AND CONFLICT PROCESSING

At a behavioural level, several robust post-error and post-conflict effects have been documented. First, it has been observed that participants are slower following an error than after a correct response (e.g., Laming, 1968; Rabbitt & Rodgers, 1977). Post-error slowing has served as evidence for an adjustment in control following an error. That is, after an error participants will shift their position on the speed-accuracy trade off to a more conservative level to avoid further errors. Specifically, this should result in slower (i.e., post-error slowing) and more accurate responses. Early investigations of error processing indeed showed that participants' response times sped up on trials before an error and slowed following an erroneous trial (Brewer & Smith, 1984; Brewer & Smith, 1989). Although post-error slowing is a very robust phenomenon, it is not always accompanied by post-error accuracy increases (e.g., Hajcak, McDonald, & Simons, 2003; Hajcak & Simons, 2008; King, Korb, von Cramon, & Ullsperger, 2010). Some authors even found post-error accuracy decreases (e.g., Fiehler, Ullsperger,

& von Cramon, 2005; Rabbitt & Rodgers, 1977). These observations question the fact that errors result in changes on the speed-accuracy trade off. Along the same line, patient studies have shown dissociations between post-error slowing and other markers of error processing (Gehring & Knight, 2000; Mathalon, Fedor, Faustman, Gray, Askari, & Ford, 2002; Modirrousta & Fellows, 2008). Based on the above, it has recently been suggested that post-error slowing can be seen as an attentional effect rather than as a control effect (Notebaert, Houtman, Van Opstal, Gevers, Fias, & Verguts, 2009; Núñez Castellar, Kuhn, Fias, & Notebaert, 2010). These authors showed that post-error slowing was only observed when errors were infrequent. When errors were frequent, post-error speeding rather than post-error slowing occurred. Slowing was even observed after irrelevant infrequent sounds (Notebaert et al., 2009). According to this view, post-error slowing is thus not related to the erroneous nature of an event, but rather to the unexpectedness that orients attention away from the current task (Notebaert et al., 2009). This was further confirmed when the described behavioural pattern was shown to be reflected in an event related potential (ERP) component related to attention (P3), and not in ERP's related to error processing (error related negativity (ERN) and feedback related negativity (FRN)) (Núñez Castellar et al., 2010).

Furthermore, a well-established finding regarding post-conflict processing is the conflict adaptation effect. This refers to reduced interference effects after conflict trials compared with no conflict trials. This effect, first described by Gratton and colleagues in the flanker task, has been interpreted as a cognitive control effect (Gratton, Coles, & Donchin, 1992). Namely, a conflict trial will require more control, resulting in a smaller interference effect on the next trial. The conflict adaptation effect has been replicated in a wide range of tasks (Simon tasks: Sturmer, Leuthold, Soetens, Schroter, & Sommer, 2002, Stroop tasks: Kerns, Cohen, MacDonald, Cho, Stenger, & Carter, 2004, and prime-target congruency effects: Kunde, 2003). However, it has been questioned whether this effect is a marker of cognitive control or the result of stimulus and response repetition and alternation effects (Hommel, Proctor, & Vu, 2004; Mayr, Awh, & Laurey, 2003; Nieuwenhuis, Stins, Posthuma, Polderman, Boomsma, & de Geus, 2006). Recently, these two opposing views were integrated in the ‘adaptation by binding’ account (Verguts & Notebaert, 2009). This account formulates cognitive control as a combination of arousal and binding processes. Moreover, an instance of conflict is seen as resulting in a higher state of arousal, causing a strengthening of the currently activated representations.

FUNCTIONAL NEURO-ANATOMY OF ERROR AND CONFLICT PROCESSING

At a neural level, a negative deflection occurring 50 ms after the onset of a response error has been well documented. This event-related potential (ERP) component is assumed to reflect conflict between concurring responses (Botvinick, Braver, Barch, Carter, & Cohen, 2001) or to signal an outcome that is worse than expected (Holroyd & Coles, 2002) and has been labeled the error related negativity (ERN). Further, the rostral cingulate zone (RCZ) has been suggested to be the main generator of the ERN (Ridderinkhof et al., 2004; Ullsperger & von Cramon, 2001). Other ERP components related to error processing are the FRN (feedback related negativity) (Miltner, Braun, & Coles, 1997) and the Pe (error positivity) (Nieuwenhuis, Ridderinkhof, Blom, Band, & Kok, 2001; Ridderinkhof, Ramautar, & Wijnen, 2009). In recent years, electrophysiological studies on error processing have expanded rigorously. However, since the neuro-anatomical research in this thesis will be conducted via fMRI methods, we will further focus on research results obtained with this measure.

Different regions of the prefrontal cortex have been associated with error and conflict processing, such as the anterior insula (e.g., Klein, Endrass, Kathmann, Neumann, von Cramon, & Ullsperger, 2007) and the lateral prefrontal cortex (e.g., Edwards, Calhoun, & Kiehl, 2012). However, the most documented region associated with error processing is situated in the posterior and medial part of the prefrontal cortex, further named the posterior medial prefrontal cortex (pMPFC). This region extends dorsally from the AC-PC line, a line connecting the anterior and posterior commissures. Anteriorly, the region extends from the VCA line, a vertical line running through the anterior commissure and perpendicular to the AC-PC line. The Brodmann areas (BAs) typically associated with the pMPFC are BA 6, BA 8, BA 9, BA 32 and BA 24 (see Figure 1). The posterior border of the pMPFC can also be marked by a subregion labeled the presupplementary motor area (preSMA). The preSMA is located in Brodmann area 6 and is distinguished by the VCA line from the more motor-related SMA (Picard & Strick, 1996). Although activation associated with response errors and response conflict extends widely along the pMPFC, the core cluster of error and conflict activity is found in the rostral cingulate zone (RCZ) (for reviews see Ridderinkhof et al., 2004; Ullsperger & von Cramon, 2004). According to Picard and Strick (1996) the RCZ extends anteriorly from the VCA line and is primarily situated in BA 32 extending ventrally in BA 24 and dorsally in BA 8 and BA 6. For an overview of the anatomical labels see Figure 1.

Whether there is an anatomical dissociation in the pMPFC between errors and conflict is still an open issue. Some studies have shown that the RCZ is activated both by errors and conflict (Carter, Braver, Barch, Botvinick, Noll, & Cohen, 1998; Kerns et al., 2004). However, others have reported a distinction in the pMPFC between errors and conflict. These latter studies showed more ventral areas related to response errors and more dorsal areas of the pMPFC related to response conflict (Braver, Barch, Gray, Molfese, & Snyder, 2001; Kiehl, Liddle, & Hopfinger, 2000; Ullsperger & von Cramon, 2001; Wittfoth, Kustermann, Fahle, & Herrmann, 2008). The meta-analysis of Ridderinkhof and colleagues (2004) suggests that while activity related to error processing tends to cluster more in BA 32 and BA 24, activity related to response conflict clusters more in BA 8. This relation is in accordance with the connections of the pMPFC to motor output. In particular, ventral parts of the pMPFC are more related to the primary motor cortex and the spinal cord whereas dorsal parts are connected to brain regions related to high-level motor cognition (Ullsperger & von Cramon, 2001; Ullsperger & von Cramon, 2004). Since errors trigger the tendency to perform the correct response it seems plausible that they are more related to regions correlated with motor output than response conflict.

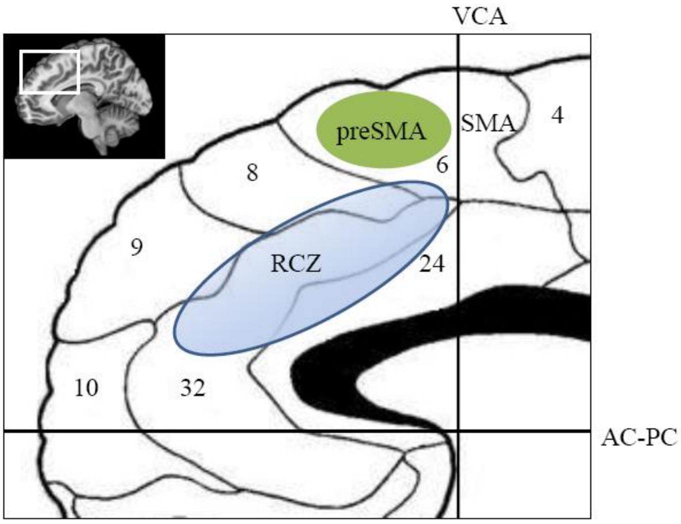

Figure 1. Midsaggital view of the pMPFC bordered by the VCA line and the AC-PC line. Two subregions of the pMPFC are indicated; preSMA is presented in green, RCZ is presented in blue. Brodmann areas are indicated with their corresponding number.

CURRENT MODELS OF ERROR AND CONFLICT PROCESSING

Different computational models have been proposed to account for the relation between errors, conflict and pMPFC activity. Hereafter, we will discuss briefly the most prominent models. The reinforcement learning theory (Holroyd & Coles, 2002) states that when outcomes are worse than expected, the mesencephalic dopamine system passes a negative reinforcement learning signal to the RCZ. These signals are then used to improve task performance. This theory predicts RCZ activity for errors and for other negative unexpected events, such as negative feedback, which has since been confirmed (Holroyd et al., 2004).

A second influential theory incorporates the role of response conflict by stating that the pMPFC, and in particular the RCZ, is involved in monitoring situations of response conflict (Botvinick et al., 2001). In other words, whenever two responses compete, the RCZ will be activated. In this view response errors are special cases of response conflict, since errors represent a conflict between the correct and the wrong response. According to the conflict monitoring theory no anatomical dissociation should be perceived between response conflict and response errors.

These two theories are combined in the error likelihood prediction account (Brown & Braver, 2005). This theory presumes that neurons in the pMPFC learn to predict the likelihood that an error will occur. Moreover, through experience the pMPFC learns to associate certain task context with the likelihood that an error will occur based on dopaminergic signals. According to this view, conflict situations will also enhance pMPFC activity by signaling increased error likelihood. However, other researchers were unable to obtain corroborative evidence for this account (Nieuwenhuis, Schweizer, Mars, Botvinick, & Hajcak, 2007).

Other theories have related pMPFC functioning to action consequences (Rushworth, Walton, Kennerley, & Bannerman, 2004) and anticipation of the need for control (Aarts, Roelofs, & Van Turennout, 2008; Fan et al., 2007; Sohn, Ursu, Anderson, Stenger, & Carter, 2000).

BEYOND THE RESPONSE LEVEL: TASK CONFLICT AND TASK ERRORS

Thus far, we have described literature concerning errors and conflict at a response level. However, conflict does not only occur at the response level but can also occur at the task level. Surprisingly, the literature on task conflict is completely separated from the literature on response conflict. Two large domains of task conflict studies can be distinguished. First, several authors have used the Stroop paradigm (Macleod, 1991; Stroop, 1935) to study processes related to task conflict. In the Stroop task participants are required to name the colour in which a word is printed while ignoring the meaning of the word (which is also a colour). In a conflict situation the meaning of the word and the colour in which it is printed will not correspond. In other words, a conflict at a task level emerges (word naming versus colour naming) (Monsell, Taylor, & Murphy, 2001). Brain regions associated with these situations of conflict are the anterior cingulate cortex (ACC) and the presupplementary motor area (preSMA) (Aarts, Roelofs, & van Turennout, 2009; Milham & Banich 2005; Woodward, Metzak, Meier, & Holroyd, 2008). It should be noted, though, that in these paradigms an influence of response related conflict cannot be ruled out entirely because the two tasks (colour naming and word naming) share the same responses (for example green and red). This issue was addressed by van Veen and Carter (2005). They also used a Stroop task but mapped two colours on one response (for example the colours red and yellow should be answered by pressing the left button). In this way they could disentangle task conflict from response conflict. More precisely, the colour naming task and the word naming task could indicate different outcomes while at a response level no conflict is apparent (the same response button is required for both tasks). These authors found a more dorsal part of the pMPFC activated by task conflict (defined as semantic conflict in their study) than by response conflict. Recent attempts showed that, by means of an ex-Gaussian distribution analysis, both types of conflict could be separated in the Stroop task (Steinhauser & Hübner, 2009).

A different class of paradigms investigating task conflict are task switching paradigms (Monsell, 2003). In these paradigms people perform two tasks randomly or in a predetermined order. A robust finding in task switching experiments is switch costs. That is, longer response times and more errors occur on task switch trials relative to task repetition trials (e.g., Monsell, 2003). In task switching studies, adaptive behaviour at the task level is thus related to the control processes needed to alternate between different tasks. Many studies have found a fronto-parietal network to be involved in task switching. This network includes the left inferior frontal junction, the left posterior superior parietal lobule (Ruge, Brass, Koch, Rubin, Meiran, & von Cramon, 2005), regions along the inferior frontal sulcus, the left intraparietal sulcus, the anterior insula (Dove, Pollmann, Schubert, Wiggins, & von Cramon, 2000), the ACC (Hyafil, Summerfield, & Koechlin, 2009) and the preSMA (Brass & von Cramon, 2002; Crone, Wendelken, Donohue, & Bunge, 2006; Rushworth, Hadland, Paus, & Sipila, 2002). Importantly, task switching does not only require resolution of conflict at the task level but also involves other processes such as goal setting and response related processes (e.g. Rubinstein, Meyer, & Evans, 2001). Therefore the task switching paradigm does not provide a pure measure of task conflict.

In sum, research on adaptation at the response level has concentrated on response conflict and response errors, typically measured in SRC tasks. Likewise, conflict at the task level has been studied with Stroop and task switching paradigms. Yet surprisingly, to our knowledge no brain imaging study has investigated the neural correlates of task errors. Thus far, only behavioural studies have addressed this issue. Steinhauser and Hübner (2006) compared switch effects after response errors with switch effects after task errors. They observed normal switch costs after response errors. However, after task errors switch benefits rather than switch costs emerged. The authors explained this finding by arguing that at the moment of a task error the wrong task is strongly activated. Consequently, subsequent task switches will actually represent task repetitions and therefore switch benefits instead of switch costs appear after a task error. In further experiments Steinhauser and Hübner (2006) confirmed that the moment of response execution is crucial for task strengthening to occur. More specifically, they demonstrated switch costs after corrected task errors but switch benefits after detected but uncorrected task errors. As mentioned above, task errors have never been investigated at the neural level. Given the extensive debate regarding the similarity/dissimilarity between response errors and response conflict this is very surprising. From a neuro-anatomical perspective it is not clear whether one would expect a dissociation of task and response errors. On the one hand, there are overlapping brain areas for response and task processing (i.e., the RCZ); on the other hand there are also brain areas uniquely related to task processing.

In **chapter two**, we will establish a design that permits us to study task and response errors in one experiment. More precisely, we will adjust a typical task switching paradigm. First, we will use univalent stimulus-response mappings instead of bivalent stimulus-response mappings. In this way we can infer from the subjects’ responses which errors were made. Second, we will include two manipulations to increase the rate of task and response errors, providing additional evidence for the theory proposed by Steinhauser and Hübner (2006). More precisely, we will replicate their behavioural dissociation and provide further knowledge concerning the role of task preparation on switch costs. However, as this was not the primary aim of the dissertation we will elaborate more on this issue in the general discussion. In **chapter three** we will use the paradigm developed in **chapter two** to study the neural correlates associated with task errors, task conflict, response errors and response conflict.

ERROR AND CONFLICT PROCESSING IN THE LABORATORY

So far, we have given an overview of studies on conflict and error processing at the task and the response level. However, nearly all these studies investigate very simple tasks that have limited ecological validity. As outlined above, conflict and/or error processing has been studied in different spatial and non-spatial compatibility tasks such as the flanker task, the Stroop task and the Simon task. Although a wide range of paradigms have been used, adaptive behaviour in such simplified tasks is restricted to very specific strategies. In the flanker task, for example, an error occurs when the central arrow is categorized incorrectly. The only possible strategy to prevent this error in subsequent trials is to pay more attention to the central arrow. However, in many real life situations an error will not only cause an increase in attention, but will also provide information that can be used to optimize further behaviour. When mastering an activity such as dancing or playing a musical instrument, it is very crucial to learn from errors, in the sense that one needs to analyze what is going wrong. This learning aspect of errors is somewhat neglected in typical laboratory tasks. As a consequence, current accounts of error monitoring might underestimate the cognitive operations following error detection.

In **chapter four** we will address this issue by examining post-error and post-conflict effects in a task that is more cognitively challenging than simple laboratory tasks, namely mental arithmetic. The results of **chapter four** can provide further insights into the debate outlined in the previous section. Classical accounts of error monitoring have described post-error slowing as an adaptive effect (e.g., Botvinick et al., 2001) whereas recent research (i.e., the orienting account) has suggested that post-error slowing can be rather seen as an attentional effect (Notebaert et al., 2009). This latter theory was developed in respect to the finding that performance does not always improve after errors. At first glance, these views seem irreconcilable; however, we believe both views can hold true dependent on the context. More precisely, when encountered with a simple laboratory task where adjustments in behaviour are very restricted, the orienting account might be better suited to explain the data. That is, we slow down due to a surprise reaction, but since we cannot do much to improve our performance we do not perform better on subsequent trials. However, when encountered with a task that is more cognitive challenging and where multiple adaptation strategies are possible, the classical theories might better explain the data pattern. Furthermore, we slow down after an infrequent erroneous event and we use the information provided by the error to change our subsequent behaviour.

OBSERVING ERRORS

In the last chapter of this dissertation we will focus on error observation. To function properly in our social world it is crucial to observe and interpret what others are doing. In particular, it can be important to identify the errors of others so that we might anticipate them.

Recent neuroscientific research has documented that the same region involved in error processing, namely the pMPFC (Ridderinkhof et al., 2004; Ullsperger & von Cramon, 2004), is also involved when observing errors in others. The activation of the pMPFC has been reported for error observation in laboratory tasks (Shane, Stevens, Harenski, & Kiehl, 2008) as well as for error observation in real life situations (Manthey, Schubotz, & von Cramon, 2003). Further, error observation both in competitive and cooperative social interactions elicits pMPFC activity (de Bruijn, de Lange, von Cramon, & Ullsperger, 2009; Newman-Norlund, Ganesh, van Schie, de Bruijn, & Bekkering, 2009). It thus seems that executing and observing errors relies on similar neural mechanisms. However, until now, it remains unclear what is the underlying reason for this shared brain system.

Shared brain activity for observation and execution has been reported for actions in general (for reviews see Rizzolatti & Craighero, 2004; Van Overwalle & Baetens, 2009). An influential theory resulting from these findings is that action understanding takes place by means of internal motor simulation (Iacoboni, Molnar-Szakacs, Gallese, Buccino, Mazziotta, & Rizzolatti, 2005; Rizzolati & Craighero, 2004; Rizolatti, Fogassi, & Gallese, 2001). If one considers error observation as a particular case of action observation, it is very tempting to assume that we also simulate each other’s errors and therefore activate the same brain region during error execution and error observation. In **chapter five** we will test this prediction by contrasting brain activity related to the observation of errors that can be simulated with brain activity related to the observation of errors that cannot be simulated. More precisely, we will use functional brain imaging while participants observe human-machine interactions in daily life that result in correct or erroneous situations. The reason for these errors can be twofold. First, the human caused the error by incorrectly operating the machine (human error). Second, the error could be caused by a malfunctioning of the machine (machine error). If the simulation hypothesis holds we should only find pMPFC activity in the human error condition and not in the machine error condition.

Beyond the distinction between machine and human errors, this latter study can provide further information considering the ventral-dorsal debate outlined in the first section. Moreover, the idea proposed regarding response errors and response conflict (i.e., since response errors are related to a motor response they will elicit more ventral parts of the pMPFC than response conflict) can be applied to the distinction between error execution and error observation. That is, since observed errors will not trigger a motor response, activity related to observed errors should be more dorsally located compared to activity related to executed errors. Based on a comparison between coordinates taken from **chapter three** and **chapter five** we are able to test this prediction.

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CHAPTER 2

PREPARING OR EXECUTING THE WRONG TASK: THE INFLUENCE ON SWITCH EFFECTS[1]

In a previous study it was proposed that executing a task leads to task strengthening. In other words, task activation at the moment of response execution determines subsequent switch effects (Steinhauser & Hübner, 2006). The authors investigated this issue by comparing switch effects after task and response errors. However, the use of bivalent stimulus-response mappings might have obscured some of the effects. Therefore, we replicated the experiment using univalent stimulus-response mappings. With this adjusted design, that overcomes some shortcomings of the original study, we were able to replicate the finding of switch benefits after task errors. Closer inspection of the data showed the importance of pre-execution processes on subsequent switch effects. In a second experiment we further elaborated on these pre-execution processes. More precisely, we investigated the effect of task preparation on subsequent switch effects. Taken together, our data extent current accounts of task switching by showing that the preparatory processes occurring before the response on trial n influence the switch cost on trial n + 1.

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[1] Desmet, C., Fias, W., & Brass, M. (in press). Preparing or executing the wrong task: the influence on switch effects. *Quarterly Journal of Experimental Psychology.*

INTRODUCTION

In task switching experiments a slowing in response times and the commission of more errors on task switch trials compared to task repetition trials is labeled the switch cost (Monsell, 2003). In a previous study Steinhauser and Hübner (2006) proposed the so called response based strengthening (RBS) account to explain the switch cost. According to this account, a strengthening of task-response associations takes place at the moment of task execution or response production and in this way affects subsequent performance. The authors found evidence for this theory by observing switch benefits instead of switch costs after task errors. In particular, when one erroneously performs task A instead of task B (for example a parity judgment instead of a magnitude judgment) the association between task A and the corresponding response is strengthened. Thus, on a subsequent trial there is an advantage of presenting task A (= switch trial) over task B (= repetition trial). On the other hand, after response errors, where the correct task is executed but the wrong response is given regular switch costs were found.

In the study of Steinhauser and Hübner (2006) (Experiment 1) single digits were presented. Two tasks were executed in a random order: a parity task and a magnitude task. A cue indicated which of the two tasks had to be performed. To dissociate task and response errors, Steinhauser and Hübner (2006) looked at the difference between congruent and incongruent stimuli. In case of a congruent stimulus the same response button is used for both tasks whereas an incongruent stimulus requires a different response for each task. For example, if the responses ‘odd’ and ‘< 5’ are mapped onto one response button, 3 is a congruent stimulus and 2 an incongruent stimulus. The logic to dissociate task errors from response errors was as follows: if participants made an error on a congruent stimulus this was considered a response error, since a task error would elicit the same response as a correct answer. On the other hand an error on an incongruent stimulus could signify both a task error and a response error. But according to Steinhauser and Hübner (2006) not much response errors will be made on these kinds of trials and so these errors were automatically considered task errors. As already mentioned, their results indicated switch benefits after errors on incongruent trials (= task errors) and typical switch costs, although not significant, after errors on congruent trials (= response errors).

Although the approach developed by Steinhauser and Hübner (2006) provides a means to study response related effects on switch costs, there are some critical points that we would like to address with the current study. First of all, a task error on a congruent stimulus cannot be detected because it requires the same response button as the correct response. All task errors on congruent stimuli were thus classified as correct responses. Second, on incongruent stimuli response errors and task errors cannot be dissociated from each other, whereas Steinhauser and Hübner (2006) considered all errors on incongruent stimuli as task errors. All response errors on incongruent stimuli were thus classified as task errors. Third, the combination of performing the wrong task and the wrong response could not be dissociated from the other error types (for example, answering ‘even’ to the stimulus ‘3’ on a magnitude task). In the experiment of Steinhauser and Hübner (2006) this would be considered a task error if ‘3’ was an incongruent stimulus and a response error if ‘3’ was a congruent stimulus. Overall, the conclusion of Steinhauser and Hübner (2006), namely that task and response errors elicit different switch effects, might be too strong considering the difficulty by which the different error types can be univocally measured in their design.

By using univalent stimulus-response mappings instead of bivalent stimulus-response mappings we were able to overcome the shortcomings outlined above. In our study every possible response was directed to one response button. This resulted in four response buttons that were divided over both hands. One hand was allocated to one task. Further, the two possible responses to a task (for example, odd and even in the Steinhauser and Hübner (2006) study) were assigned to two fingers of the corresponding hand, which resembles the method used in Meiran and Daichman (2005). Consequently, on a certain trial each of the four response buttons corresponded unequivocally with one sort of response (a correct response, a response error, a task error or a combination of a task and a response error). Thus, in contrast to Steinhauser and Hübner's (2006) design we were able to measure the exact number of task and response errors.

In addition, we introduced two additional factors to increase the number of task and response errors. First, during the trial itself an extra transition cue (which indicated a repetition or a switch in respect to the task under execution) could be presented. The timing of this transition cue was manipulated such that we could control the number of task errors made. In our design a task error can thus be defined as not being able to change to the correct task in time. Second, to increase the response error rate we presented flanker stimuli on both sides of the target stimulus. More response errors were expected on incongruent flanker trials compared to congruent flanker trials.

The investigation of task errors is not only useful to study response related modifications of switch effects. It also bridges the gap between research on error processing and research on task switching. More precisely, task error research could lead to a gain of insight in the combination of these two domains by for example investigating neural dissociations between different error types (Desmet, Fias, Hartstra, & Brass, 2011) or dissociations between post-error adjustments (Steinhauser & Hübner, 2008). However, behavioural studies on task errors that were reported so far all use the approach described above to disentangle task errors from other error types. Considering the timely issue of this topic, our study provides further information about the methods that can be used to study the relation between cognitive control and task related processes.

EXPERIMENT 1

METHOD

Participants. Eighteen subjects with normal or corrected-to-normal vision participated in this study. All participants were students at the University of Ghent and received 10 euros for participation.

Material. Stimuli were presented on a 17-inch computer screen. The viewing distance was about 50 cm. The response times were registered by a Pentium 4s PC.

Stimuli and tasks. The experiment was conducted using Tscope software (Stevens, Lammertyn, Verbruggen, & Vandierendonck, 2006). Stimuli were presented on a black background. The target stimulus was centered on the middle of the screen (total outline: 1.3 cm x 0.4 cm) and always consisted of three letters. These letters were combinations of the letters L and R (outline: 0.7 x 0.4 cm) and could be printed in green or in yellow with this restriction that the two outside letters were always identical. The word ‘kleur’ (colour) or ‘letter’ (letter) preceded target presentation and served as a primary cue. A secondary task cue could appear after target presentation and consisted of a horizontal or a vertical ellipse centered on the target. The cues and the ellipses (outline: 1.5 cm x 3 cm for the vertical ellipses and 3 cm x 1.5 cm for the horizontal ellipses) were both presented in white.

Participants had to perform one of two tasks in each trial; a letter or a colour task. The letter cue and the colour cue indicated the letter task and the colour task respectively. The presentation of both cues was randomized over all trials. During the letter task participants had to decide if the middle letter of the target was an L or and R. In the colour task the middle letter of the target had to be classified as green or yellow. On one third of the trials subjects had to make a task switch after target presentation in respect to the primary cue. This switch was indicated by a vertical ellipse appearing around the target. For example: if the letter cue is presented and the middle letter of the target is a green R surrounded by a vertical ellipse, then the correct answer would be green instead of R. To control for the appearance of the ellipse also horizontal ellipses were presented. If a horizontal ellipse was presented, participants were instructed to do the task as was indicated by the primary cue. Further, to reduce waiting strategies in one third of all trials no ellipses were presented (no ellipse trials). To induce task errors and to control their number we adjusted the timing of the appearance of the ellipse following a staircase procedure. If participants made a correct response when a vertical ellipse was presented (within switch trial), the timing of the ellipse was delayed by 20 ms on the next trial. If participants made a task error on a trial with a vertical ellipse, the ellipse on the subsequent trial was presented 20 ms earlier. On the first trial the ellipse appeared 250 ms after the presentation of the target. The earliest point at which the ellipse could appear was 5 ms after target presentation. Note, that this procedure resembles that of the stop change paradigm. By varying the timing of the change signal delay (timing between the target presentation and the change signal) the chance of correctly performing the second task can be manipulated (for an overview see Verbruggen, Schneider, & Logan, 2008). After a response error, a combination error or a too slow response, the timing of the ellipses was not adjusted. The outside letters of the target served as flanker stimuli. In half of the trials these flankers yielded the same response as the middle letter (congruent flanker condition). In the other half of the trials the flankers yielded a different response than the middle letter (incongruent flanker condition). Congruence or incongruence of the flankers always regarded the task specified by the last cue. For example: under the execution of the colour task two outside green letters and one middle yellow letter represent an incongruent flanker situation, independent from the identity of the letters presented (L or R). The 16 possible combinations of flanker and target occurred equally often. See Figure 1 for an example of a trial sequence.

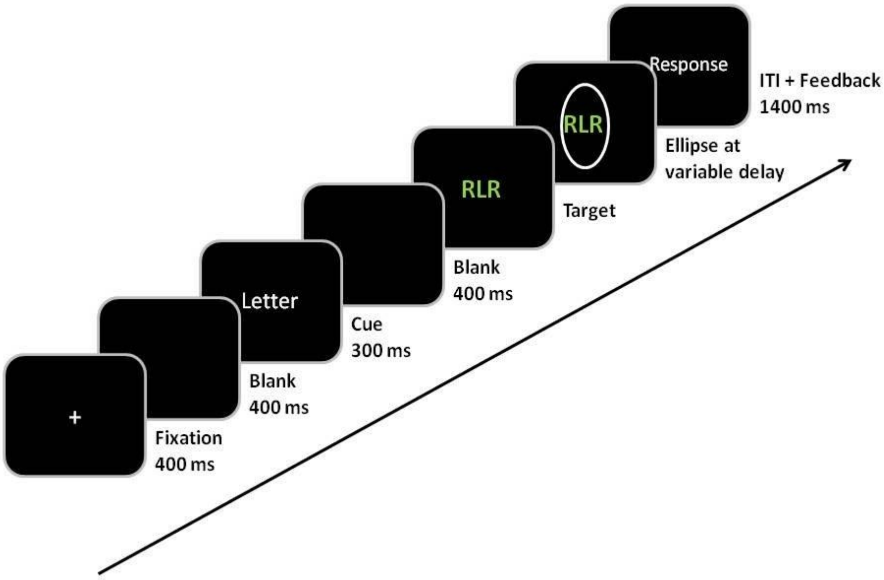

Figure 1. Example of a trial sequence in Experiment 1.

Responses were given by the index and the middle finger of the left and the right hand. One task always corresponded to one hand. Further the letter L always corresponded to the left finger and the letter R always corresponded to the right finger. The mapping of the hands to the tasks and of the colours to the fingers was counterbalanced across participants. By using these univalent stimulus-response mappings we could disentangle three different types of errors: response errors, task errors and combination errors. A response error corresponds to a response with the correct hand but with the wrong finger of that hand. This means that the correct task is performed but that the wrong response is given. For example, if the colour task has to be executed and a green letter is presented, a response error would be ‘yellow’. Second, a task error corresponds to a response with the wrong hand but with the correct finger of that hand. This means that you are in the wrong task but nevertheless give the correct response in that task. For example, if the letter task has to be executed and a green R is presented, a task error equals ‘green’. A third type of errors that we defined were combination errors. This corresponds to a response with the wrong hand and with the wrong finger. For example if a green R is presented during the letter task, a combination error would correspond to the response ‘yellow’.

Design and procedure. The independent variables were within trial transition (no ellipse = no ellipse trial, horizontal ellipse = within repetition trial, vertical ellipse = within switch trial), flanker (congruent or incongruent trial) and between trial transition (between repetition or between switch trial). This last variable indicated whether on two subsequent trials the same task (between repetition trial) or a different task (between switch trial) had to be executed. Considering these three variables, we obtained 12 different cells. Every cell was repeated 48 times during the experiment. In total participants received 576 experimental trials.

The experiment started with a practice phase of 24 trials in which the ellipse did not appear. This was done to practice the stimulus-response mappings. After this practice phase a short break was presented. In a second practice phase of 72 trials the ellipses were introduced. During these practice phases the response deadline was 3000 ms. In the last 48 trials of the second practice phase the response deadline was determined for each participant individually. This was done by taking the mean response time on incongruent flanker trials.

Each trial started with the presentation of a fixation cross for 400 ms. After the presentation of a blank screen of 400 ms the primary cue appeared for 300 ms. A blank screen followed for 400 ms, then the target was presented until subjects responded or until the response deadline had passed. Between the appearance of the target and the response deadline the ellipse appeared (except for the no ellipse trials). This ellipse stayed on the screen together with the target until a response was given. After the disappearance of the target, feedback was provided for erroneous trials and for too slow responses. The words ‘FOUT’ (wrong) or ‘TE TRAAG’ (too slow) stayed then on the screen for 400 ms. Further, the words ‘TE TRAAG’ (too slow) were accompanied by an acoustic stimulus. In the cases where no feedback was provided a blank screen was included for 400 ms. After 1000 ms the next trial was presented. The experiment lasted for one hour. In the middle of the experiment a short break was inserted.

RESULTS

Overall error rates. The mean error rate was 25%, consisting of 12% task errors, 10% response errors and 3% combination errors. Trials where participants responded before the appearance of the ellipse (0.44%), before the appearance of the target (0.01%), or after the response deadline (8%) were discarded from the analysis. This resulted in an exclusion of 8.5% of all trials.

As expected the task error rate was higher on within switch trials compared to the other trial types, $F(1,17) = 51.93$, $p < 0.001$ (5% (SD = 0.05) in no ellipse trials, 6% (SD = 0.05) in within repetition trials and 25% (SD = 0.09) in within switch trials). The number of response errors was similar over the three levels of the within trial transition variable, $F(2,34) = 1.64$, $p = 0.21$ (10% (SD = 0.06) in no ellipse trials, 10% (SD = 0.06) in within repetition trials and 12% (SD = 0.07) in within switch trials).

In contrast to what could have been expected the number of response errors was equal for congruent and incongruent flanker trials ($F(1,17) = 0.37$, $p = 0.55$). (Also the number of task errors was constant over congruent and incongruent flanker trials, $F < 1$.)

To summarize, the number of task errors was effectively manipulated by the within trial transition variable, whereas the flanker manipulation did not affect the number of response errors. However, there was an effect of the flanker manipulation on response times. That is, faster responding occurred on congruent flankers compared to incongruent flankers, $F(1,17) = 10.77$, $p < 0.01$. So, although the flankers did not affect response errors, they did affect participants' performance. Nevertheless, we obtained a sufficient rate of response errors to examine the effect of response errors on subsequent trials. Probably the response errors resulted from the use of a response deadline and the general difficulty of the task.

Effects of task and response errors on subsequent trials. Error rates as well as mean response times were analyzed by two-way ANOVAs with repeated measures on the variables TRIAL TYPE N-1 (correct trial, task error trial and response error trial) and BETWEEN TRIAL TRANSITION (between repetition trial and between switch trial). In addition to the exclusion criteria cited above, we also discarded trials subsequent to trials where participants responded before the appearance of the ellipse or before the appearance of the target. Furthermore, the first trial of the experiment and the first trial after the pause were excluded from the analysis. This resulted in a mean exclusion of 9% of all trials.

Error rates. In accordance with the results of Steinhauser and Hübner (2006) the interaction between TRIAL TYPE N-1 and BETWEEN TRIAL TRANSITION was significant, $F(2,34) = 5.63$, $p < 0.01$ (see Figure 2). There was a reliable switch cost after correct trials, $F(1,17) = 31.99$, $p < 0.001$. After task errors we observed switch benefits, $F(1,17) = 4.55$, $p < 0.05$, and after response errors there were small but non significant switch costs, $F < 1$.

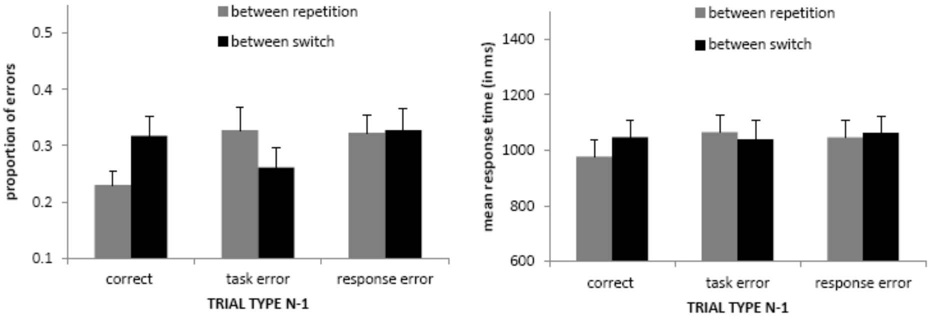

Figure 2. Between trial transition effects following correct responses, task errors and response errors measured on errors and response times.

Because of our manipulation the task error rates are large in within switch trials but small in no ellipse trials and in within repetition trials. As a result the above pattern could change according to the different types of the within trial transition variable. In the following analysis we tested whether the data pattern remained the same for the three different types of the within trial transition variable. We computed a three-way repeated measures ANOVA on the variables WITHIN TRIAL TRANSITION N-1 (no ellipse trial, within repetition trial and within switch trial) TRIAL TYPE N-1 (correct trial, task error trial and response error trial) and BETWEEN TRIAL TRANSITION (between repetition trial and between switch trial). The three-way interaction was marginally significant, $F(4,68) = 2.37$, $p = 0.06$. Planned comparisons showed that for every level of the within trial transition variable there were reliable switch costs after correct responses (for no ellipse trials: $F\ (1,17) = 15.44$, $p < 0.01$; for within repetition trials: $F\ (1,17) = 18.91$, $p < 0.01$ and for within switch trials: $F\ (1,17) = 18.26$, $p < 0.01$). Further the switch benefits after task errors were significant for no ellipse trials and within repetition trials but not for within switch trials (for no ellipse trials: $F(1,17) = 12.25$, $p < 0.01$; for within repetition trials: F $(1,17) = 10.22$, $p = 0.01$ and for within switch trials: $F < 1$). Finally, the switch costs after response errors did not reach significance in any of the three levels of the within trial transition variable (for no ellipse trials: $F < 1$; for within repetition trials: $F < 1$ and for within switch trials: $F < 1$). See Figure 3. The two-way interaction between TRIAL TYPE N-1 and BETWEEN TRIAL TRANSITION was significant for no ellipse trials ($F(2,34) = 11.15$, $p < 0.001$) and within repetition trials ($F(2,34) = 7.69$, $p < 0.01$) but not for within switch trials ($F(2,34) = 1.71$, $p = 0.20$).

Some task errors were the result of very fast responding. As a result, these errors could be perceived differently by the subjects and therefore elicit different results. To investigate this matter, we divided the task errors according to the time between ellipse occurrence and response. A time interval of 250 ms or less was defined as fast. Using this cut-off resulted in a comparable amount of trials in fast and slow cells ($F < 1$). We performed a repeated measures ANOVA on the variables TASK ERROR N-1 (fast versus slow) and BETWEEN TRIAL TRANSITION (between repetition trial and between switch trial). The variables did not interact, $F < 1$, indicating that the absence of switch benefits after task errors was not due to the timing of the ellipse on the previous trial. Main effects of BETWEEN TRIAL TRANSITION ($F < 1$) and TASK ERROR N-1 ($F(1,17) = 1.35$, $p = 0.26$) were not significant.

Response times. The mean response time was 1026 ms (measured from target presentation). Although we obtained a significant interaction between TRIAL TYPE N-1 and BETWEEN TRIAL TRANSITION on trial N, F $(2,34) = 4.29$, $p < 0.05$, the switch benefits after task errors were not significant, F $(1,17) = 2.02$, $p = 0.17$. Significant switch costs emerged after a correct response, $F(1,17) = 41.36$, $p < 0.001$. Finally, there were no significant switch costs after response errors, $F < 1$. See Figure 2.

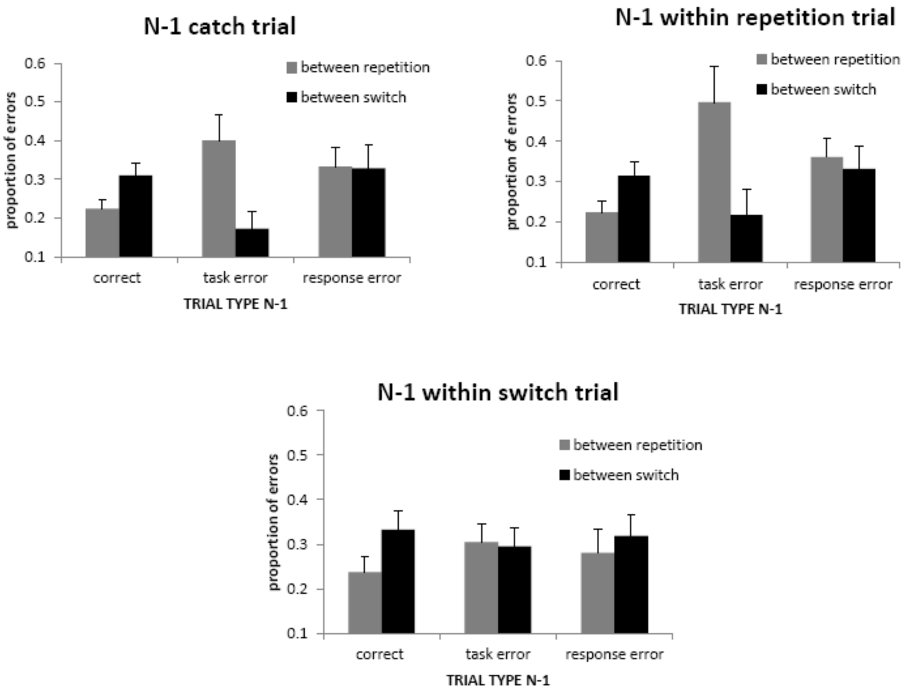

Figure 3. Between trial transition effects following correct responses, task errors and response errors on no ellipse trials, within repetition trials and within switch trials measured on error rates.

DISCUSSION EXPERIMENT 1

The aim of the present study was to replicate the dissociation between task and response errors with an adjusted design that unequivocally allows dissociating task errors from response errors. Instead of using bivalent stimulus-response mappings we used univalent stimulus-response mappings. In this way we could disentangle the different types of errors (namely; task errors, response errors and a combination of both errors) in a more straightforward manner. Second, we used a procedure to increase the rate of task and response errors. The number of task errors was effectively manipulated by the within trial transition variable. Although we failed to induce response errors by our flanker manipulation, we found a sufficient response error rate. In general, we replicated the results of Steinhauser and Hübner (2006). That is, we found an interaction between TRIAL TYPE N-1 (correct response, response error and task error) and BETWEEN TRIAL TRANSITION (between repetition trial and between switch trial) on error rates. More specifically, after the execution of a task error switch benefits instead of switch costs emerged on the subsequent trial. Although the pattern for response times mirrors that of the error rates we did not obtain significant switch benefits after task errors. In the study of Steinhauser and Hübner (2006) no significant effects were found for response times either. Originally, the authors attributed this finding to the use of a response deadline that might have obscured the data. However in a further paper, where they did not use response deadlines, they did not obtain significant interactions (only marginal) for response times either (Steinhauser & Hübner, 2008). Nevertheless, as in our study, the direction of the response time pattern resembled that of the error rate pattern, so there was no sign of a speed-accuracy trade off.

An additional important difference between our study and the study of Steinhauser and Hübner (2006) is that we used feedback whereas they did not. In spite of the feedback we still observed switch benefits after the execution of task errors. This is highly in line with the RBS account proposed by Steinhauser and Hübner (2006). According to this account it is not the activation of the task at the end of the trial but the task activation at the moment of an overt response that will influence the next trial. They supported this hypothesis by showing that switch benefits after task errors still emerged when participants had to indicate whether they made an error or not. Similarly, in our experiment the feedback, or the knowledge that one executed the wrong task (given that participants knew to what error type the feedback referred), did not overrule the effects emerging from the error execution itself. To summarize, overall we replicated the findings of

Steinhauser and Hübner (2006) and seemingly found further support for the RBS account.

Surprisingly, the two-way interaction between TRIAL TYPE N-1 and BETWEEN TRIAL TRANSITION on error rates was not significant after within switch trials. In other words, the switch benefits disappeared after trials where task errors were elicited, and thus where most task errors were made. We could thus say that the observations of Steinhauser and Hübner (2006) did not emerge on trials where two tasks were cued (one by the primary cue and one by the ellipse). This indicates that the task that was not executed (indicated by the primary cue) also influenced switch costs. Moreover, it seems that both task indications (primary and secondary cue) lead to switch effects, respectively switch benefits and switch costs, and as such cancel out switch effects on the next trial. This would suggest that not only the task that was related to the executed response leads to switch effects but that also the task that was not executed has an influence on switch effects. In task switching literature, the role of response execution on subsequent switch costs has been stressed (Philipp, Jolicoeur, Falkenstein, & Koch, 2007; Schuch & Koch, 2003; Verbruggen, Liefooghe, & Vandierendonck, 2006). Also the RBS account considers response execution a necessary condition to obtain subsequent switch effects. However, the fact that pre-execution influences switch costs does not necessarily contradict the RBS account. More precisely, according to the RBS theory, task strengthening occurs at the moment of response execution proportional to the task activation of the executed task. Strong task activation will lead to strong strengthening of this particular task and vice versa. Probably, task activation will be less strong when two tasks are presented, compared to situations where only one task occurs. Consequently, the absence of switch effects in double task trials could be explained by minor task strengthening due to smaller task activation.

To further investigate the influence of pre-execution on switch effects, we conducted an additional experiment in which we compared switch effects after trials in which two tasks were indicated compared to trials in which only one task was indicated. Instead of offering the secondary task indication at a variable delay after target presentation we decided to offer the secondary task indication at a fixed short (60 ms) or long delay (700 ms) before presentation of the stimulus. In this way, the variability caused by the variable delay of the transition variable is reduced. A similar approach was taken in an fMRI study of Brass and von Cramon (2004) investigating the role of task preparation. To unravel effects of cue processing and task preparation they applied a double cue to task mapping. In other words, two cues were allocated to one task and two other cues were allocated to the other task. Before the presentation of the stimulus two cues were consecutively presented. In this way three different trial types emerged; the same cue appeared twice (switch none), two different cues appeared but they indicated the same task (switch cue) and two different cues, indicating different tasks appeared (switch task). Interestingly, the difference between switch task and switch cue trials, signifies a switch to the other task while controlling for cue related processes. If we find a reduction in between-trial switch costs after switch task trials compared to switch cue trials, this would confirm our hypothesis and signify that pre-execution processes already influence switch effects on the next trial. Since we replicate the method used in Brass and von Cramon (2004), we decided to use their tasks (parity and magnitude) and stimuli (numbers) instead of the letter and colour task of Experiment 1.

EXPERIMENT 2

METHOD

Participants. Nineteen subjects with normal or corrected-to-normal vision participated in this experiment. All participants were students at the University of Ghent and received 10 euros in exchange for participation.

Apparatus. Stimuli were presented on a 17-inch computer screen. The viewing distance was about 50 cm. The response times were registered by a Pentium 4s PC.

Stimuli and tasks. The experiment was conducted using Tscope software (Stevens et al., 2006). Stimuli were presented in white on a black background. The target stimulus was centered on the middle of the screen and was a number ranging from 20 to 40 (except for the number 30). According to the experimental condition one or two cues were offered before target presentation. Cues consisted of four different figures; diamond, square, triangle and inverted triangle.

Participants had to perform two number tasks; a parity (Is the target stimulus odd or even?) and a magnitude task (Is the target stimulus larger or smaller than 30?). The diamond and the triangle indicated the magnitude task. The square and the inverted triangle indicated the parity task.

Four experimental conditions were defined. In two fifths of the trials only one cue was shown before target presentation (one cue condition). In the switch none condition two identical cues were presented before target presentation. In the switch cue condition two different cues indicating the same task were offered (for example a diamond and a triangle). Finally, in the switch task condition two different cues indicating different tasks were presented (for example a diamond and a square). Switch none, switch cue and switch task trials were equally divided over three fifths of the trials. The task of the participant was to categorize the target number according to the last offered task cue. The transition of tasks between trials was also balanced. In other words, over the whole experiment the amount of between task repetitions and between task switches was the same (between task transitions are defined as the transition between the tasks that have to be executed). In half of the trials a short cue target interval was presented (60 ms), in the other half of the trials a long interval was presented (700 ms). In total participants received 1200 experimental trials.

Responses were given by the index fingers of the left and the right hand. The responses belonging to one task were divided over the two buttons. The four different stimulus-response mappings were balanced across participants.

Procedure. The experiment started with a practice phase of 60 trials. The first 20 trials were one cue trials. The subsequent 20 trials included all experimental conditions. However, participants received 7000 ms to fulfill a trial. Finally, the last 20 practice trials were identical to the experimental trials.

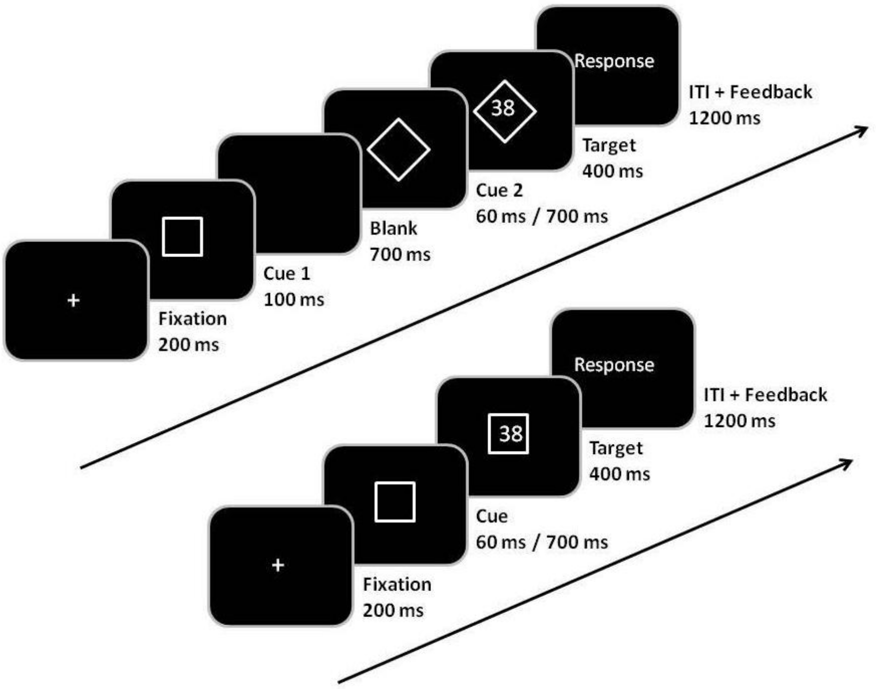

Figure 4. Example of a switch task (above) and a one cue trial (below) in Experiment 2.

Each trial started with the presentation of a fixation cross for 200 ms. Then a cue appeared for 100 ms. After the presentation of a blank screen of 700 ms the second cue (except for one cue trials) appeared for 100 ms. After 60 ms (short CTI) or 700 ms (long CTI) the target was presented for 400 ms. From the presentation of the target onwards participants received 2000 ms to respond. After erroneous responses the word ‘FOUT’(wrong) was presented on the screen for 200 ms. After a too slow response the words ‘TE TRAAG’ (too slow) appeared. In the cases where no feedback was provided a blank screen was included for 200 ms. After an interval of 1000 ms the next trial started. The experiment lasted for one hour. Two small breaks were inserted. See Figure 4 for an overview of the trial sequence.

RESULTS

The mean response time was 932 ms (SD = 163) and the mean error rate was 16% (SD = 7%).

Response times. Switch costs were analyzed by a repeated measures ANOVA on the variable CONDITION N-1[2] (one cue, switch none, switch cue and switch task). Too slow responses, the first experimental trial, every first trial after a break and the first trial following these conditions were discarded. On the current trial only correct one cue trials were included. Also, on trial N-1 only correct trials were included. In this way 26% of all trials were effectively used in the analysis. The main effect of CONDITION N-1 was significant, indicating that switch costs altered after different trial types, $F(3,54) = 3.56$, $p < 0.05$. We further

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[2] Note that we also manipulated the interval between the last cue and the stimulus (CTI). Since this variable did not influence further switch costs, we did not include the variable in the reported ANOVA. However, the results concerning the CTI manipulation are presented in Appendix A.

investigated this finding by comparing switch costs after the two crucial conditions namely, switch cue trials and switch task trials. The switch cost was larger after switch cue trials than after switch task trials, *F*(1,18) = 8.43, *p* < 0.01. See Figure 5.

Error rates. Analogous to the analysis on response times we compared switch costs after the different trial types by conducting a repeated measure ANOVA on the variable CONDITION N-1. However, it seems that switch costs measured on error rates do not differ after the different conditions as the effect of CONDITION N-1 did not reach significance, *F*(3,54) = 1.42, *p* = 0.25. On error rates we did thus not replicate the effect of preparation on the switch cost. See Figure 5.

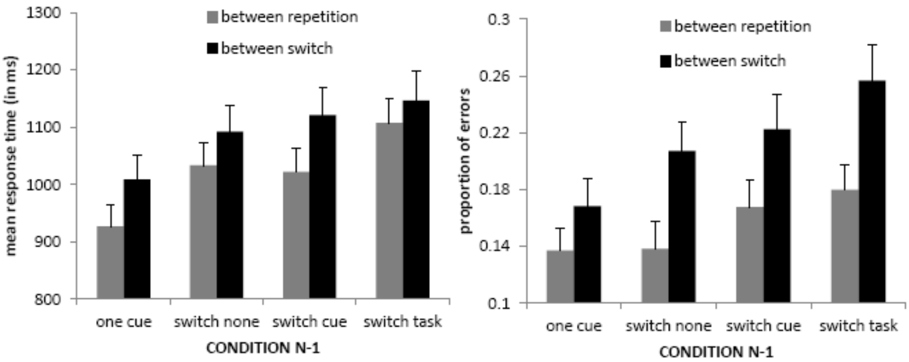

Figure 5. Between trial transition effects following one cue, switch none, switch cue and switch task trials on response times and error rates.

DISCUSSION EXPERIMENT 2

In line with our prediction we found that when on the previous trial two tasks are prepared switch costs are reduced. In other words, tasks that are not overtly executed can influence further switch effects. However, as outlined in the discussion of Experiment 1, our data do not deny the triggering role of response execution. In other words, response execution might be needed to exert the influence of task preparation.

GENERAL DISCUSSION

By using a paradigm that allows to unequivocally disentangle task errors from response errors, we largely replicated the findings of Steinhauser and Hübner (2006) of switch benefits after task errors. This finding provides further evidence for the RBS account. Even with univalent stimulus-response mappings switch benefits were found after task errors. However this effect was restricted to trials where only one task is indicated. In trials where two tasks were indicated no switch effects emerged after task errors. This led us to formulate the hypothesis that a task that is not executed might also influence switch costs on the next trial. To study this issue in more detail we performed a second experiment. We compared switch costs after double cue trials. According to our hypothesis, we found that switch costs were reduced after trials in which two different tasks were cued compared to trials where only one task was cued. We thus argue that pre-execution processes, and in particular task preparation, can influence performance on subsequent trials. In a way our data thus extend the RBS account, by demonstrating the influence of task preparation on task activation. In other words, we investigate the conditions that lead to task activation and as such influence the strengthening of a task.

Pre-execution processes should thus not be neglected in task switching research. Moreover, we believe that the double cue method used in our experiments can shed more light on the particular role that is attributed to response execution. For example, in the RBS account it is stated that response execution is needed for task strengthening. Also, research using go-nogo methods have labeled response execution a necessary condition for subsequent switch costs (Philipp et al., 2007; Schuch & Koch, 2003). However, using a double cue method leads to some observations that need further attention regarding this issue. First, one can consider the double cue trials from Experiment 2 as a mixture of two trial types. More precisely, double cue trials can be seen as a sequence of a trial consisting of one cue and a trial consisting of a cue and a target (trial 1: cue, trial 2: cue-target). We observed worse performance on switch task trials (e.g., trial 1: parity, trial 2: magnitude-target) compared to switch cue trials (e.g., trial 1: parity, trial 2: parity-target) ($F(1,18) = 7.25$, $p < 0.05$). If we consider the first cue as a separate trial we might say that we have an indication that switch effects emerge after trials on which no response was given and thus where no strengthening could have taken place (i.e., trials where only a cue appeared). However, since the time between consecutive cues was relatively small, subjects probably did not perceive the first cue as a separate trial. Interestingly, in another experiment of Brass and von Cramon (2002), effects of trials in which only a cue appeared (cue only) were studied in more detail. There, cue only presentations were considered as separate trials. That is, a fixation cross separated these trials from the next and from previous trials. Further, the cue only trial lasted for 2000 ms. Although this study was an fMRI experiment and was only ran on 13 subjects, we reanalyzed the behavioural data in light of the current hypothesis. Consistent with our hypothesis, we found (marginal) switch costs after cue only trials. On short CTI conditions we obtained a switch cost of 41 ms after a cue only trial, ($F(1,12) = 4.40$, $p = 0.06$). On long CTI conditions the switch cost after cue only trials was not significant (-3 ms, $F < 1$). This observation was also recently found in a study of Lenartowicz, Yeung and Cohen (2011). These authors showed that while no-go trials lead to a reduction of switch costs, trials in which only a cue was presented did evoke switch costs.

A second argument is provided by neuroimaging data. In the studies of Brass and von Cramon (2002) and Brass and von Cramon (2004) it is shown that preparation without execution (as measured in cue only trials and switch task trials) already evoke general preparation related brain regions. In particular, these regions mirror those found for switch versus repeat trials in regular single cue trials. In other words, the cognitive control network is already involved during task preparation, irrespective of task execution. If preparation only has an indirect influence via the increase or decrease of task specific activation one would expect only task specific activation during mere task preparation.

CONCLUSION

In sum, in Experiment 1 we replicated the original findings of Steinhauser and Hübner (2006). More precisely, with an adjusted design that remedies some of the shortcomings of the procedure used by Steinhauser and Hübner (2006) we could replicate the dissociation between response and task errors. In addition, we found that pre-execution processes, and in particular task preparation, might play an important role on the switch cost. Future research should thus further elaborate on the role of different stages of task processing.

Finally, as already mentioned in the introduction we would like to stress the importance of research on different error types. Although in this study, different error types were only used as a method to investigate switch effects, our results indicate that task errors can be dissociated from response errors. More specific, a task error leads to a benefit while a response error leads to a cost. This implies that task errors lead to an improvement of the wrong behaviour. Steinhauser and Hübner (2008) already addressed this question and showed that an additional slow-acting mechanism (error induced inhibition) overcomes the negative consequences from task error learning in slow trials. In this way subsequent behaviour can be optimized and learning from task errors is not impossible.

ACKNOWLEDGEMENTS

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APPENDIX A

RESPONSE TIMES

A repeated measures ANOVA on the variables CTI N-1 (short CTI and long CTI) and TYPE N-1 (one cue, switch none, switch cue and switch task) revealed a non significant main effect of CTI N-1, $F < 1$. As expected from the analysis reported in the manuscript, the main effect of TYPE N-1 was significant, $F(3,54) = 3,85$, $p < 0.05$, with reduced switch costs on switch task trials compared to switch cue trials, $F(1,18) = 9.58$, $p < 0.01$. The interaction between CTI N-1 and CONDITION N-1 did not reach significance, $F < 1$. In particular, paired comparisons showed that the CTI N-1 variable did not alter the switch costs after switch task trials, $F < 1$ or the difference in switch costs between switch cue and switch task trials, $F < 1$.

ERROR RATES

Switch costs were again analyzed by means of a repeated measures ANOVA on the variables CTI N-1 (short CTI and long CTI) and TYPE N-1 (one cue, switch none, switch cue and switch task). None of the main effects (CTI N-1: $F(1,18) = 1.33$, $p = 0.26$, TYPE N-1: $F(3,54) = 1.47$, $p = 0.24$) nor the interaction($F < 1$) reached significance. Further, the switch effects after switch task trials ($F(1,18) = 1.52$, $p = 0.23$), or the difference in switch costs between switch cue and switch task trials were not changed by the CTI N-1 variable, $F < 1$.

CHAPTER 3

ERRORS AND CONFLICT AT THE TASK LEVEL AND THE RESPONSE LEVEL[1]

In the last decade research on error and conflict processing has become one of the most influential research areas in the domain of cognitive control. There is now converging evidence that a specific part of the posterior medial prefrontal cortex (pMPFC), the rostral cingulate zone (RCZ), is crucially involved in the processing of errors and conflict. However, error related research has primarily focused on a specific error type, namely response errors. The aim of the present study was to investigate whether errors on the task level rely on the same neural and functional mechanisms. Here we report a dissociation of both error types in the pMPFC: whereas response errors activate the RCZ, task errors activate the dorsal frontomedian cortex. Although this last region shows an overlap in activation for task and response errors on the group level, a closer inspection of the single subject data is more in accordance with a functional anatomical dissociation. When investigating brain areas related to conflict on the task and response level, a clear dissociation was perceived between areas associated with response conflict and with task conflict. Overall, our data support a dissociation between response and task levels of processing in the pMPFC. In addition, we provide further evidence for a dissociation between conflict and errors both at the response level and at the task level.

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[1] Desmet, C., Fias, W., Hartstra, E., & Brass, M. (2011). Errors and conflict at the task and the response level. *Journal of Neuroscience, 31*(4), 1366-1374.

INTRODUCTION

There is a long lasting debate regarding the functional organization of the posterior medial prefrontal cortex (pMPFC) in adaptive control (Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004; Ullsperger & von Cramon, 2004). The term pMPFC refers to the part of the medial frontal cortex that extends from the presupplementary motor area (preSMA) anteriorly and dorsally from the anterior cingulate sulcus including parts of the anterior cingulate cortex (Ridderinkhof et al., 2004; Ullsperger & von Cramon, 2004). Several studies have reported a dorsal-ventral distinction in this region with more ventral parts being involved in error processing and more dorsal parts involved in conflict resolution (Braver, Barch, Gray, Molfese, & Snyder, 2001; Kiehl, Liddle, & Hopfinger, 2000; Ullsperger & von Cramon, 2001; Wittfoth, Kustermann, Fahle, & Herrmann, 2008). From a neuro-anatomical perspective such a dissociation seems plausible because ventral parts of the pMPFC are more related to the primary motor cortex and the spinal cord whereas dorsal parts are connected to brain areas related to high-level motor cognition (Ullsperger & von Cramon, 2001; Ullsperger & von Cramon, 2004). Since response errors require a response change it is reasonable to assume that they rely on motor-related brain areas while response conflict cannot be resolved by giving another response and therefore should rely on brain areas involved in higher level adaptive processes. So far, however, error and conflict research has focused primarily on the response level while greatly ignoring the more abstract task level. Interestingly, recent conflict research suggests that increasing the level of abstractness leads to a shift of conflict related brain activity in the anterior direction. In particular, it seems that posterior parts of the pMPFC are related to response conflict while anterior parts are related to other forms of conflict such as conflict between decisions and strategies (Kouneiher, Charron, & Koechlin, 2009; Pochon, Riis, Sanfey, Nystrom, & Cohen, 2008; Venkatraman, Rosati, Taren, & Huettel, 2009).

The aim of the current study is to manipulate the level of abstractness both for errors and conflict by investigating errors and conflict on the task and the response level. Task related control processes have been investigated with the so called task switching paradigm (Monsell, 2003). Here participants have to alternate between different task representations. However, most task switching research has exclusively focused on accurate performance. Only few studies have addressed erroneous performance or task errors (Steinhauser & Hübner, 2006; Steinhauser & Hübner, 2008; Steinhauser, 2010). By studying both errors and conflict at the response and task level our design permits us to combine the dimension of abstractness (response level and task level) with the dimension of control (conflict and errors). This raises the interesting possibility to compare task related processing with response related processing for errors (task errors versus response errors) and conflict (task conflict versus response conflict). In addition, the design enables us to compare error with conflict related processing within each level of abstractness (response errors versus response conflict / task errors versus task conflict).

Based on the above mentioned literature, we expect to find dissociations between response conflict and response errors. Furthermore, we also expect a dissociation between response conflict and task conflict. However, as regards the activity for task errors and its relation to response errors, two alternative hypotheses can be formulated. On the one hand, one can argue that both response and task errors signal the need for adaptive processes. From this perspective both types of errors should activate similar brain regions. On the other hand, one can argue that the type of adaptive behaviour required after both errors is completely different. While response errors require an adaptation of the motor output, task errors require more abstract adaptive processes. From this perspective, one would predict task and response errors to rely on different brain areas.

METHOD

PARTICIPANTS

21 participants (16 females) participated in this study (mean age = 22.8 years, SD = 2.5 years). All were right handed as was measured by the Edinburgh Inventory (Oldfield, 1971). 25 euro could be earned in exchange for participation. All participants gave written informed consent and had no history of neurological disorders. Ethical approval was given by the Medical Ethical Review Board of the Ghent University hospital.

STIMULI AND TASKS

The experiment was implemented using Tscope software (Stevens, Lammertyn, Verbruggen, & Vandierendonck, 2006). Stimuli were presented on a black background. The target stimulus was centered on the middle of the screen and consisted of a coloured letter. The letter could be printed in green or in yellow and was either an L or an R. The word ‘colour’ or the word ‘letter’ preceded target presentation and served as task cue for the colour task and the letter task respectively. The presentation of both cues was randomized over all trials. During the letter task participants had to decide if the letter on the screen was an L or and R. In the colour task the letter had to be classified as green or as yellow. In the task change condition a secondary task cue could appear after target presentation and consisted of a vertical ellipse centered on the target. The cues and the ellipse were both presented in white.

Three types of trials were presented. First, to induce task errors a secondary task cue was presented after target presentation. This secondary task cue consisted of an ellipse and always indicated a task switch in respect to the primary task cue or the word cue. For example, a green R surrounded by an ellipse following the letter cue should be answered with green and not with R. Further, we adjusted the timing of the presentation of the ellipse to a staircase procedure. On the first ellipse trial (= task change trial) the ellipse appeared 250 ms after target presentation. If participants made a correct response, then the presentation of the ellipse on the next trial was delayed by 20 ms. If, on the other hand, participants made a task error on a task change trial, the ellipse was presented 20 ms earlier on the next trial. In this way the chance of making a task error on a task change trial was about 50 percent. The earliest time point at which the ellipse could appear was 5 ms after target presentation. Second, to induce response errors we exchanged the appeared target with a different target after a certain delay. The second target differed from the first one according to the relevant stimulus dimension. For example, under execution of the colour task a green R would change into a yellow R. To perform the trial correctly participants had to respond to the stimulus that appeared the latest. As in the task change trials the timing of the target exchange was adjusted to a staircase algorithm. This means that after a correct response on a stimulus change trial, a target change on the next trial occurred 20 ms later. Whereas, after a response error on a stimulus change trial the target change on the next stimulus change trial appeared 20 ms earlier. Again, the earliest time point at which the change could occur was 5 ms after the first target presentation and the time interval between first and second presentation on the first trial was 250 ms. Note that this method resembles that of the stop change paradigm. By varying the timing of the change signal delay (time between the target presentation and the change signal) the chance of correctly performing the second task can be manipulated (for an overview see Verbruggen, Schneider, & Logan, 2008). Third, to reduce waiting strategies we also offered catch trials. In these trials no ellipses or changes of target were presented. For an overview of the different trial types see Figure 1. Responses were given by the index and the middle finger of the left and the right hand by response button boxes that were placed on the right and left upper leg. Similar to Meiran and Daichman (2005), we used univalent stimulus-response mappings. This means that we mapped every possible response to one effector. More specifically, we allocated each task to a different hand and then allocated the index and the middle finger of both hands to a different response. Further, the L response always corresponded to the left finger and the R response always corresponded to the right finger. The mapping of the hands to the tasks and of the colours to the fingers was balanced across participants. In this way every possible response, and likewise every possible error, was mapped onto a different effector. This allows inferring from the subject's responses which type of error was made (Meiran & Daichman, 2005). A response error corresponds to a response with the correct hand but with the wrong finger of that hand. This means that the correct task is performed but that the wrong response is given. For example, the response yellow to a green letter under the execution of the colour task would correspond to a response error. A task error corresponds to a response with the wrong hand but with the correct finger of that hand. This equals a correct response to the wrong task. For example, the response green to a green R under the execution of the letter task is considered a task error. Note that a response with the wrong hand is not automatically classified as a task error. One could also respond with the wrong hand and with the wrong finger. This would represent a combination of a response and a task error. For example, the response yellow to a green R under the execution of the letter task would correspond to this combined error.

DESIGN AND PROCEDURE

In total there were 4 blocks. Every block consisted of 80 experimental trials and 8 null events. The null events consisted of a blank screen presented for 4500 ms. The 80 experimental trials were divided over 32 task change trials, 32 stimulus change trials and 16 catch trials. The presentation of trials was randomized so that the amount of task repetitions and task switches between trials was the same over all trials.

Participants received a first training phase outside the scanner. This training phase was divided over four blocks. In the first three blocks respectively only catch trials, task change trials and stimulus change trials were offered. During the final block all trial types were then intermixed. The second training phase took place in the scanner while the anatomical scan was taken. During this phase a mixture of all trial types was immediately presented.

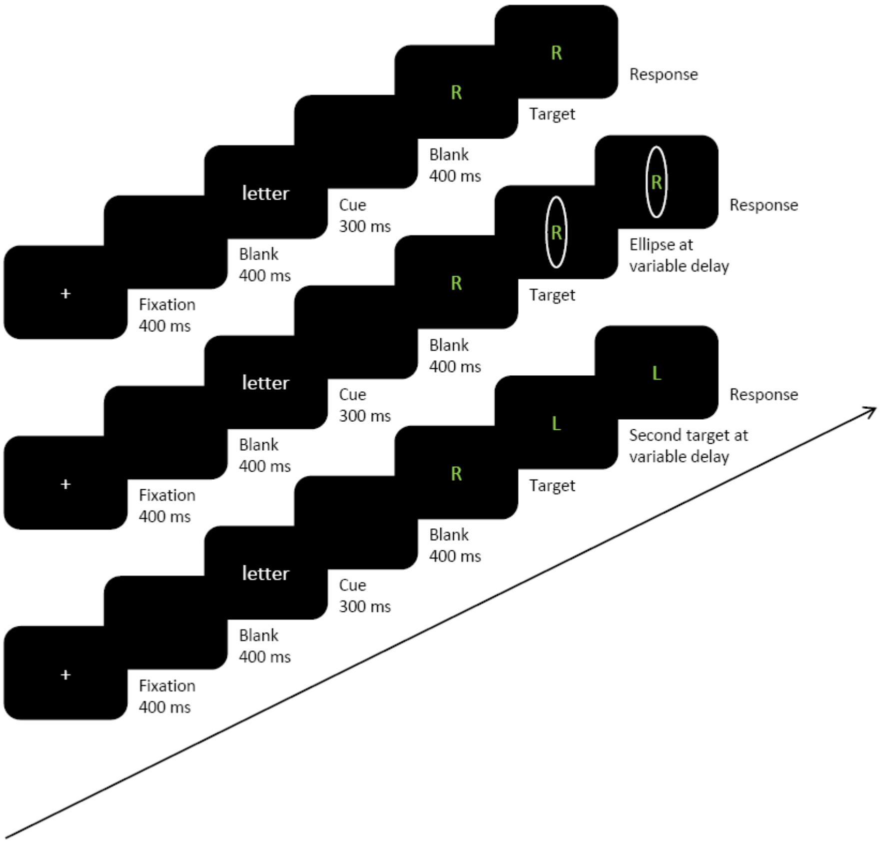

Figure 1. Sequence of the three different trial types. From top to bottom: catch trials, task change trials and stimulus change trials. Two different tasks have to be performed; classifying the colour of the letter as green or as yellow or classifying the letter as an R or an L. All trial types start with the presentation of a task cue. This task cue indicates the colour task (the word ‘colour’ appears) or the letter task (the word ‘letter’ appears). Four response buttons are used. They are allocated to the index and middle finger of the left and right hand. One task was allocated to one hand and the L response was

always allocated to the left finger of the corresponding hand. In catch trials the task indicated by the task cue has to be applied on the stimulus at the moment of stimulus presentation. In task change trials we tried to elicit task errors by presenting a task change signal after stimulus presentation. This task change signal indicates a task switch in respect to the primary cue. In the figure, the correct response for the task change trial is thus green and not R. The delay between the stimulus and the task change signal was adjusted to a staircase algorithm. As a result participants should make about 50% task errors in the task change trials. In stimulus change trials we tried to elicit response errors by presenting a stimulus change after the first stimulus presentation. Participants should try to respond to this changed stimulus and not to the first presented stimulus. In the figure the correct response for the stimulus change trial is thus L and not R. We also adjusted the delay between the primary and secondary stimulus to a staircase algorithm so that the percentage of response errors would be around 50%.

Each trial started with a variable jitter interval of 0, 500, 1000 or 1500 ms. Then a fixation cross was presented for 400 ms. After a blank screen presentation for 400 ms the cue appeared. After a cue stimulus interval of 700 ms the target appeared until participants responded or until the deadline of 3000 ms had passed. Between the presentation of the target and the response deadline an ellipse or a changed stimulus could appear. Likewise the target presentation, the ellipse and the changed stimulus stayed on the screen until participants responded or until 3000 ms had passed. During the practice phase feedback was provided after an erroneous answer (the word ‘FOUT’ (wrong) appeared on the screen for 400 ms), during the experiment itself no feedback was provided. Only after too slow responses the words ‘TE TRAAG’ (too slow) appeared on the screen for 400 ms. The sequence of the different trial types is shown in Figure 1.

FMRI METHODS

The experiment was carried out on a 3T scanner (Siemens Trio) using an 8-channel radiofrequency head coil. Subjects were positioned head first and supine in the magnet bore. First, 176 high-resolution anatomical images were acquired using a T1-weighted three-dimensional MPRAGE sequence (TR = 2530 ms, TE = 2.58 ms, image matrix = 256 ×256, FOV = 220 mm, flip angle = 7º, slice thickness = 0.90 mm, voxel size = 0.9 ×0.86 × 0.86 mm (resized to 1×1×1 mm)). Whole brain functional images were collected using a T2*-weighted EPI sequence, sensitive to BOLD contrast (TR = 2000 ms, TE =35 ms, image matrix = 64 × 64, FOV = 224 mm, flip angle = 80º, slice thickness = 3.0 mm, distance factor = 17%, voxel size 3.5 × 3.5 × 3 mm, 30 axial slices). A varying number of images were acquired per run because of the self-paced initiation of trials. All data were analyzed using SPM5 (http://www.fil.ion.ucl.ac.uk/spm/software/spm5/). To account for T1 relaxation effects each EPI sequence started with two dummy scans. First, all functional images were spatially realigned using rigid body transformation. After the realignment they were slice-time corrected using the first slice as a reference. The structural image of each subject was co registered with their mean functional image. Further, all functional images were normalized to the Montreal Neurological Institute (Montreal, Quebec, Canada) T1 template. The images were resampled into 3.5 mm^3 voxels and spatially smoothed with a Gaussian kernel of 8 mm (full-width at half maximum). A high pass filter of 128 seconds was applied during fMRI data analysis. To correct for multiple comparisons we used the program AlphaSim (afni.nimh.nih.gov/afni/doc/manual/AlphaSim). This program determines the probability of a false positive detection from the frequency count of cluster sizes, using Monte Carlo simulations. The program determined that a cluster size of 22 contiguous voxels, considered that $Z > 3.1$ ($p < 0.001$ uncorrected), corresponded to a corrected $p < 0.05$ level. Consequently, in the results section we only report activated clusters of minimum 22 voxels. Statistical analyses were performed using the general linear model implemented in SPM5. We distinguished task errors, response errors and correct trials for the three experimental conditions (catch trials, task change trials and stimulus change trials), resulting in 9 regressors. Because we wanted to dissociate different error types, the moment of response execution (correct response or error) was used as a main event of interest in the general linear model. Both a canonical hemodynamic response function (HRF) and the first time derivative were modeled on the moment of response for each trial. Six regressors defining head movement were also included in the model to account for residual movement effects. We computed contrast images by comparing the parameter estimates for the regressors containing the canonical HRF.

RESULTS

BEHAVIOURAL RESULTS

Two participants (2 females) were excluded from the analyses. Their mean error rates (66% and 64%) differed more than two SD's from the overall mean.

To investigate the effect of both staircase algorithms we compared the percentage of errors and correct trials in the different trial types. In task change trials we observed 42% correct trials (SD = 8), 47% task errors (SD = 8), 5% response errors (SD = 3) and 6% combination errors (SD = 4). In stimulus change trials there were 48% correct trials (SD = 2), 2% task error trials (SD = 2), 46% response errors (SD = 6) and 1% combination errors (SD = 1). In catch trials we observed 85% correct trials (SD = 9), 3% task error trials (SD = 4), 11% response errors (SD = 8) and 1% combination errors (SD = 2) (see Figure 2). Overall, the percentage of combination errors was very small (mean = 3%, SD = 3) and even in the task change trials the percentage only rose to 6%. This shows that participants did not just switch hands and guessed one out of the two responses during task change trials, otherwise the percentage of combination errors would have been higher.

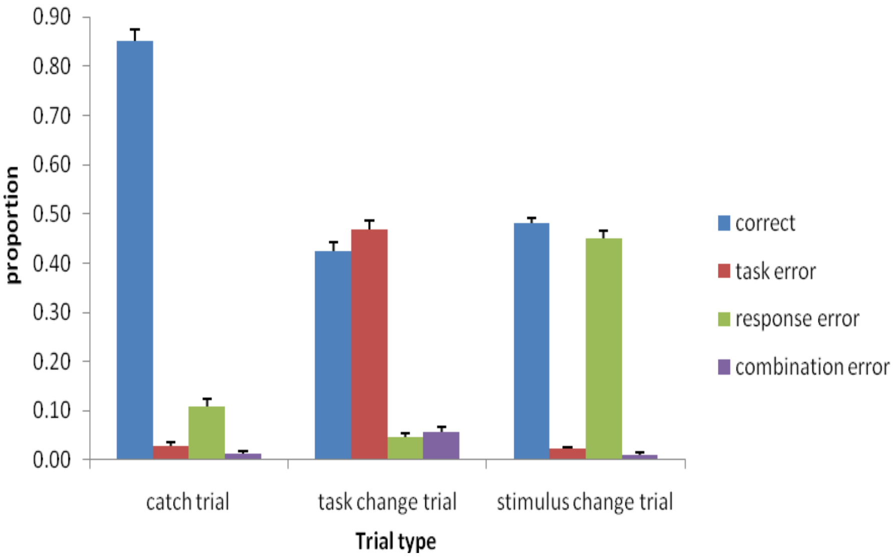

Figure 2. Proportion of correct answers, task errors, response errors and combination errors on catch trials, task change trials and stimulus change trials. Bars represent standard errors across subjects.

The mean reaction time over conditions and over participants was 754 ms (SD = 155). We performed a repeated measures ANOVA analysis on the factors TRIAL TYPE (task change trials and stimulus change trials) by TYPE OF RESPONSE (correct, error) on reaction times. Note that the error corresponds to task errors in the task change trials and to response errors in the stimulus change trials. The analysis showed that correct answers (1229 ms) were performed slower than errors (576 ms) ($F(1,18$ = 263.61, $p < 0.001$) and that task change trials (1014 ms) were performed slower than stimulus change trials (792 ms) ($F(1,18) = 146.03$, $p < 0.001$). These effects are logically explained by the fact that erroneous responses are a consequence of an insufficient processing of the secondary cue or secondary stimulus and are thus faster than correct responses where the secondary cue or stimulus is more deeply processed. More interestingly the interaction between both factors also reached significance ($F(1,18) = 79.49$, $p < 0.001$). It seems that it is harder to perform a correct response under a task change trial (1432 ms) than a correct response under a stimulus change trial (1026 ms). In other words, overcoming task conflict seems to be more difficult than overcoming response conflict, see Figure 3.

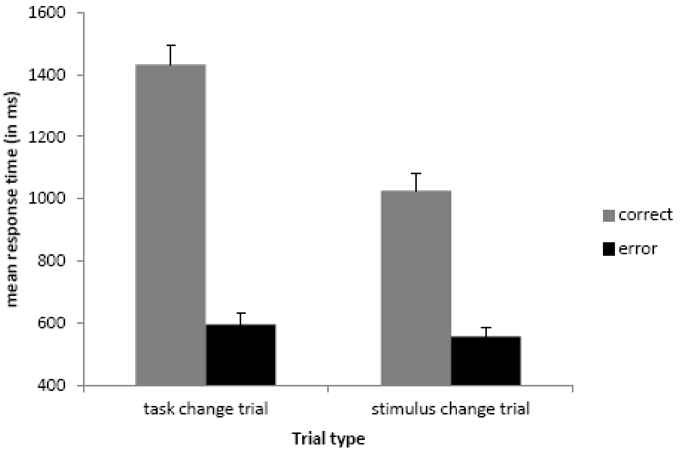

Figure 3. Interaction of trial type (task change trial, stimulus change trial) by type of response (correct, error) on mean response times in ms. Bars represent standard errors across subjects.

In the previous analysis it is difficult to interpret reaction times because the staircase algorithm is applied on the investigated trials and therefore can interfere with the observed effects. In the following analyses we investigated if these effects remained on the subsequent trial. We performed a repeated measures ANOVA analysis on the factors PREVIOUS

TRIAL TYPE (trial n-1 task change trials and trial n-1 stimulus change trials) by PREVIOUS TYPE OF RESPONSE (trial n-1 correct, trial n-1 error) on reaction times and error rates. Further, we only included correct catch trials on the current trial. Thus, in these analyses the staircase algorithm cannot interfere with the observed effects since there are no ellipses or changes of stimuli on catch trials. Participants were slower after correct trials (806 ms) than after erroneous trials (678 ms), $F(1,18) = 11.87$, $p < 0.01$. The phenomenon of post-error speeding has been reported before. Notebaert and colleagues (2009) showed that reaction times after an error are dependent on the proportion of errors in the experiment. In experiments where the frequency of occurrence of an error is high and therefore not surprising (as in our experiment) post-error speeding instead of post-error slowing is observed (Notebaert, Houtman, Van Opstal, Gevers, Fias, & Verguts, 2009). Furthermore, participants were slower after task change trials (797 ms) than after stimulus change trials (688 ms), $F(1,18) = 10.81$, $p < 0.01$. The two way interaction between PREVIOUS TRIAL TYPE (trial n-1 task change trials and trial n-1 stimulus change trials) and PREVIOUS TYPE OF RESPONSE (trial n-1 correct, trial n-1 error) was marginally significant, $F(1,18) = 4.05$, $p = 0.06$. The effects of the difficulty of overcoming task conflict (trial n-1correct task change trial: 895 ms) in comparison to response conflict (trial n-1 correct stimulus change trial: 716 ms) seemed thus to persist in the next trial, see Figure 4. The same analysis on error rates revealed only a main effect of PREVIOUS TRIAL TYPE, $F(1,18) = 10.57$, $p = 0.004$, participants made more errors after a task change trial (21%) than after a stimulus change trial (14%). The main effect of PREVIOUS TYPE OF RESPONSE and the interaction between both factors did not reach significance (F’s < 1).

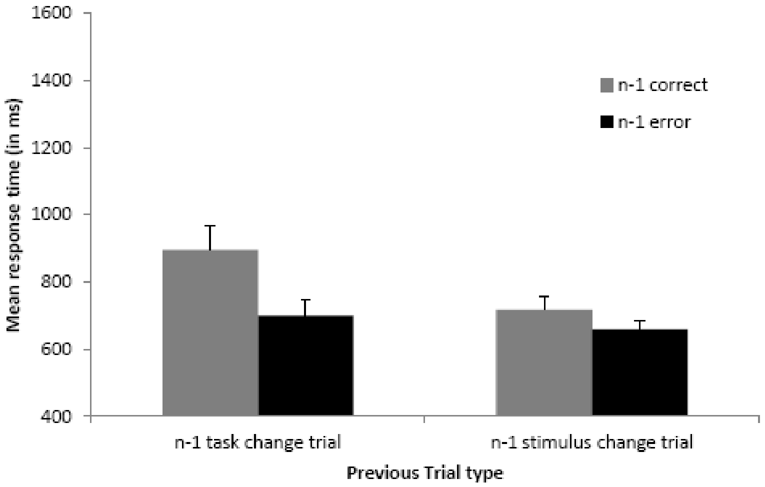

Figure 4. Interaction of previous trial type (trial n-1 task change trial, trial n-1stimulus change trial) by previous type of response (trial n-1correct, trial n-1error) on mean response times in ms on catch trials. Bars represent standard errors across subjects.

FMRI RESULTS

Error related activation. The first part of the analyses concentrated on whole brain contrasts revealing brain areas associated with response errors and brain areas associated with task errors. To this aim we selected task change trials to compute task error contrasts and stimulus change trials to compute response error contrasts. The logic underlying the composition of the contrasts was equal for both situation; we subtracted correct trials from error trials.

The first contrast subtracted task change correct trials from task change task error trials and should thus show areas associated with task errors. Brain activity in the pMPFC was found. More precisely, the contrast revealed activation in a region located more dorsal and anterior than the RCZ (as defined by Picard & Strick, 1996) which we will label as the dorsal frontomedian cortex (dFMC) (MNI coordinates, 6 39 54). Further, we found activation in the right inferior parietal lobe (rIPL, 57 -48 48).

The second contrast aimed at revealing response error regions and subtracted stimulus change correct trials from stimulus change response error trials. Again, we found pMPFC activity. It seems that an area somewhat anterior to the rostral cingulate zone (RCZ, 6 51 30) was activated along with the dorsal frontomedian cortex (dFMC, 6, 27, 54). Further, we observed activity in the right middle temporal gyrus (rMTG, 57 -66 3), and the right insula (rINS, 39, 21, -9) Brain activity related to task and response errors is shown in Figure 5 (see Table 1 for an overview of all related activations per contrast).

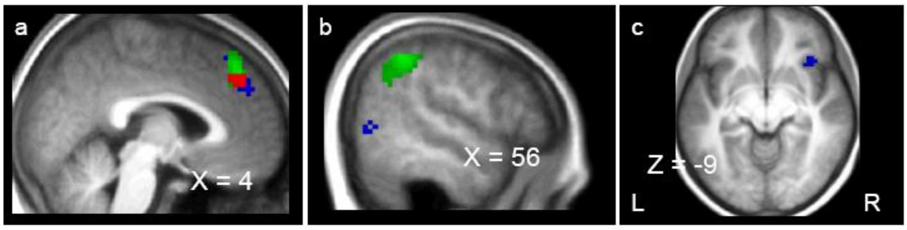

Figure 5. Response error (blue) and task error (green) related activation superimposed on anatomical slices averaged across subjects. Response error activation is related to the contrast: stimulus change trials: response errors – correct trials. Task error activation is related to the contrast: task change trials: task errors – correct trials. (a) Activation for response and task errors in the pMPFC (MNI coordinates of maximal random-effect Z scores, blue: x, y, z = 6, 51, 30 , Z = 3.87 and x, y, z = 6, 27, 54, Z = 4.13, green: x, y, z = 6, 39, 54, Z = 4.45). Overlapping activation is presented in red (MNI coordinates of maximal random effects Z scores, x, y, z = 3, 45, 39, Z = 3.43). (b) Activation in the MTG for response errors and in the IPL for task errors (MNI coordinates of maximal random effects Z scores, blue: x, y, z = 57, -

66, 3, Z = 3.87, green: x, y, z = 57, -48, 48, Z = 4.56). (c) Activation in the INS for response errors (MNI coordinates of maximal random effects Z scores, x, y, z = 39, 21, -9, Z = 3.46).

Table 1. MNI Coordinates of Whole Brain Contrasts

	Peak coordinates	Z-score	Extent
Task error (task change trials: task error – correct)			
Dorsal frontomedian cortex (dFMC)	6 39 54	4.45	99
Inferior parietal lobe (IPL)	57 -48 48	4.56	108
Response error (stimulus change trials: response error – correct)			
Dorsal frontomedian cortex (dFMC)	6 27 54	4.13	32
Rostral cingulate zone (RCZ)	6 51 30	3.87	44
Insula (INS)	39 21 -9	3.46	22
Middle temporal gyrus (MTG)	57 -66 3	3.87	39
Conjunction task error and response error			
Dorsal frontomedian cortex (dFMC)	3 45 39	3.43	28
Response conflict (correct stimulus change trial- correct catch trial)			
Inferior frontal junction (IFJ)	-45 18 27	3.52	69
Rostral cingulate zone (RCZ)	-6 30 39	3.70	35
Middle frontal gyrus (MFG)	42 27 42	4.43	69
Frontomarginal sulcus (FMS)	-36 54 6	4.03	115
Task conflict (correct task change trial – correct catch trial)			
Presupplementar motor area (preSMA)	-9 15 57	4.03	56
Middle frontal gyrus (MFG)	42 54 18	4.09	49
Inferior frontal gyrus (IFG)	-51 15 -3	4.02	22
Premotor cortex (PM)	-39 9 60	5.09	947
Inferior frontal junction (IFJ)	-39 15 24	4.75	
Dorsolateral prefrontal cortex (DLPFC)	-39 45 3	4.94	

Conjunction task conflict and response conflict			
Middle frontal gyrus (MFG)	-36 51 27	4.46	173
Inferior frontal junction (IFJ)	-39 15 24	3.62	69

To answer one of the main questions of the research, namely do task and response errors activate different or overlapping regions, we performed a conjunction analysis on the two above contrasts. This analysis shows activated voxels in the response error AND in the task error contrast at a group level. As expected from the results described above, we observed a significant overlap in the pMPFC (3 45 39) after applying the conjunction analysis. In addition, we examined if there were activations in the pMPFC uniquely related to one type of error. Therefore we masked both error contrasts with each other at a threshold of $p < 0.001$. For example, to investigate unique activation for task errors we took the task error contrast (task change task error – task change correct) and masked it with the response error contrast (stimulus change response error – stimulus change correct). The results showed that there was unique brain activity related to task errors in the dorsal part of the pMPFC (6, 36, 60) whereas unique brain activation related to response errors was located more ventral and more anterior in the pMPFC (3, 48, 33), (cluster size = 19 voxels).

From the above analyses it seems that there is an overlap in the pMPFC between both error activations but that there is also unique activation belonging to response errors and unique activation belonging to task errors. In a final analysis we investigated if the overlap between both error activations could be identified for each participant individually. It could well be that the observed overlap is an artifact of the conjunction analysis. More precisely, in the conjunction analysis the overlap in activation is defined as the overlap between the group contrast for response errors and the group contrast for task errors. Therefore, individual variation is no longer taken into account. It is thus possible that none of the subjects show an overlap in task and response errors while at a group level this overlap is significant. Considering that the cingulate sulcus shows a lot of anatomical variability between subjects (Paus et al., 1996; Pujol et al., 2002; Yücel et al., 2001) this hypothesis seems plausible. In order to investigate overlapping and unique brain activation at an individual level we first defined a region of interest in the pMPFC. This region was defined as follows: we took the three peak voxels of the task and response error activation in the pMPFC (MNI coordinates response errors: 6, 51, 30; 6, 27, 54; task errors: 6, 39, 54) and drew a sphere of 20 mm around each of these coordinates. The range of the region stretched for the x-axis from -14 to 26, for the y-axis from 7 to 71 and for the z-axis from 10 to 74. Next, for each participant a conjunction and two masking analyses were performed in this region of interest. The conjunction and masking analyses were equal to the ones described in the group results, namely a conjunction between the task error and the response error contrast, a masking of the response error contrast with the task error contrast and a masking of the task error contrast with the response error contrast. The threshold was set low (p = 0.05 uncorrected) in order to observe activation for every subject and no smoothing was applied. To be able to compare the activations across participants, we will express the number of activated voxels in percentages for each participant. The percentage of activation for task errors was calculated by dividing the number of voxels that were uniquely activated by task errors by the total amount of error activation in the mask. The percentage of activation for response errors was calculated by dividing the number of uniquely activated voxels for response errors by the total amount of error activation in the mask. Finally, the percentage of overlapping activation was calculated by dividing the number of voxels activated in the conjunction analysis by the total amount of error activation in the mask. Overall, the mean percentage of unique task error activation was larger (55%) than the mean percentage of unique response error activation (37%), although not significantly ($t(18) = 1.56$, $p = 0.14$). If we take a closer look at Table 2 we see that 11 participants showed more activation for task errors than for response errors. More importantly, the overall percentage of overlap between both error types was quite small (8%). Further, it seems that this figure was mainly based on a relatively strong overlap for only 4 participants (overlap > 15%) (See Table 2). In order to check that the absence of overlap was not due to an inflation of noise, we replicated the above analysis with a higher threshold ($p < 0.01$). From Table 2 it is clear that we replicated the above findings; the overall amount of overlap was very small, 3%. Only one participant showed an overlap higher than 15%. The percentage of unique task error activation (63%) was higher than the amount of unique response error activation (33%), $t(18) = 2.28$, $p = 0.04$. Further, 12 participants showed higher task error activation than response error activation. While 1 participant showed low activation for task errors (2%), 6 participants showed a low activation for response errors (< 15%).

Table 2. Percentage of Activation Uniquely Related to Task Errors, Uniquely Related to Response Errors and Percentage of Overlap of Both Errors for $p = 0.05$. Between brackets are the values corresponding to a p value of 0.01.

Participant	Total number of activated voxels	Task error in percentage	Response error in percentage	Overlap in percentage
1	425 (93)	43 (40)	49 (58)	8 (2)
2	403 (179)	90 (94)	8 (5)	2 (1)
3	236 (68)	86 (100)	11 (0)	3 (0)
4	552 (170)	3 (2)	97 (98)	0 (0)
5	319 (67)	36 (37)	62 (63)	3 (0)
6	145 (23)	54 (57)	45 (43)	1 (0)
7	428 (173)	80 (95)	8 (3)	12 (2)
8	90 (12)	81 (83)	18 (17)	1 (0)
9	1204 (699)	68 (83)	13 (9)	19 (8)
10	223 (48)	26 (21)	73 (79)	2 (0)
11	227 (41)	23 (51)	73 (49)	4 (0)

12	340 (67)	38 (49)	56 (49)	7 (1)
13	147 (32)	48 (44)	49 (53)	3 (3)
14	655 (261)	88 (92)	5 (5)	7 (3)
15	694 (284)	61 (75)	21 (17)	19 (8)
16	78 (14)	62 (86)	38 (14)	0 (0)
17	222 (55)	73 (80)	22 (18)	5 (2)
18	948 (390)	27 (34)	45 (51)	28 (15)
19	1147 (792)	61(80)	3 (1)	36 (19)

Conflict related activation. In the second part of the analyses we investigated brain areas related with response and task conflict. Both conflict contrasts (response and task conflict) were designed by contrasting correct conflict trials with correct no-conflict trials. More precisely, we subtracted correct catch trials from correctly executed stimulus change trials and correctly executed task change trials respectively for response and task conflict. Because these contrasts also subtract two different screen displays a lot of sensory-related brain activity, for example in the occipital lobe showed up. Therefore we only report the activated frontal areas.

The first contrast aimed to look at response conflict. Therefore, we subtracted correct catch trials from correct stimulus change trials. An area slightly anterior to the left inferior frontal junction (lIFJ,-45 18 27), the RCZ (RCZ, -6 30 39), the right middle frontal gyrus (rMFG, 42 27 42), and an area in the left frontopolar cortex, the frontomarginal sulcus (lFMS,-36 54 6) were activated.

The second contrast aimed at revealing regions related to task conflict. We subtracted correct catch trials from correct task change trials. The presupplementary motor area (preSMA, -9 15 57) and the right middle frontal gyrus (rMFG, 42 54 18) were activated along with a region stretching from the premotor cortex (PM, -39 9 60) over an area somewhat anterior to the left inferior frontal junction (lIFJ, -39 15 24) ending in the left dorsolateral prefrontal cortex (lDLPFC, -39 45 3). Figure 6 shows brain activity related to response conflict and task conflict.

Finally, we wanted to see if response and task conflict subserved overlapping brain activation. Because task change trials and stimulus change trials comprise two completely different types of events, we will not directly compare them. However, likewise as in the error contrasts we performed a conjunction analysis on the two above contrasts (task and response conflict). This should also reveal which brain regions are commonly activated by response and task conflict. The conjunction analysis showed that the left middle frontal gyrus (lMFG, -36 51 27), and the left IFJ (lIFJ, -39 15 24) showed activation for both conflict levels.

INTEGRATING CONFLICT AND ERRORS

In the final part of the analyses we will compare conflict and error activations for the two different levels of abstractness. In other words, we will relate response conflict with response error activation and task conflict with task error activation. To this aim we performed two conjunction analyses.

First, we performed a conjunction analysis between the response error contrast and the response conflict contrast. No significant activations emerged. This means that in our study there was no significant overlap between response conflict activity and response error activity. If we take a closer look at the coordinates in the pMPFC related to response conflict and response errors we can conclude that response conflict triggers regions located more dorsal and more posterior than response errors.

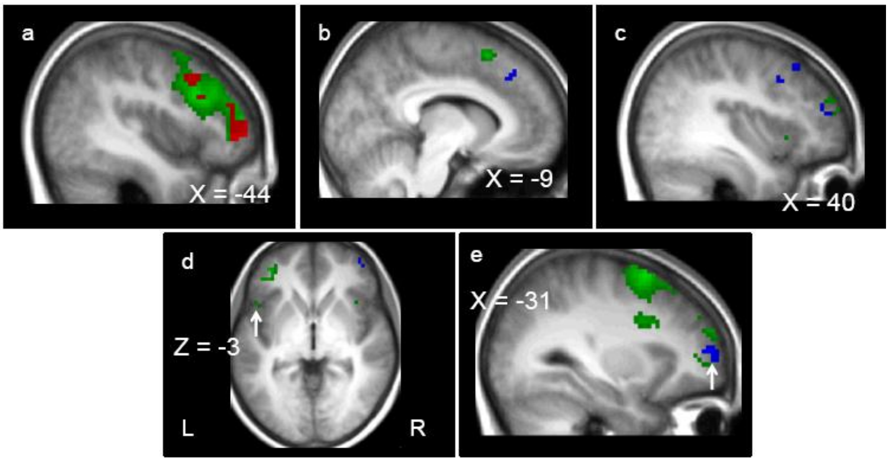

Figure 6. Response conflict (blue) and task conflict (green) related activation superimposed on anatomical slices averaged across participants. Response conflict is related to the contrast stimulus change correct trials – catch correct trials. Task conflict is related to the contrast task change correct trials – catch correct trials. (a) Activation in the PM, IFJ and DLPFC for task errors (MNI coordinates of maximal random-effect Z scores, green: x, y, z = -39, 9, 60, Z = 5.09, x, y, z = -39, 15, 24, Z = 4.75 and x, y, z = -39, 45, 3, Z = 4.94) and activation in the IFJ for response errors (MNI coordinates of maximal random-effect Z scores, blue: x, y, z = -45, 18, 27, Z = 3.52). Overlapping activity is represented in red in the IFJ and the MFG (MNI coordinates of maximal random-effect Z scores, x, y, z = -39, 15, 24 , Z = 3.62 and x, y, z = -36, 51, 27, Z = 4.46). (b) Activation in the preSMA for task conflict and in the RCZ for response conflict (MNI coordinates of maximal random-effect Z scores, green: x, y, z = -9, 15, 57, Z = 4.03 and blue: x, y, z = -6, 30, 39, Z = 3.70). (c) Activation in the MFG for task conflict and for response conflict (MNI coordinates of maximal random-effect Z scores, green: x, y, z = 42, 54, 18, Z = 4.09 and blue: x, y, z = 42, 27, 42, Z = 3.43). (d) Activation in the IFG for task conflict (MNI coordinates of maximal random-effect Z scores, x, y, z = -51, 15, -3 , Z = 4.02). (e) Activation in the frontopolar cortex for response conflict (MNI coordinates of maximal random-effect Z scores, x, y, z = -36, 54, 6, Z = 4.03).

In addition, we performed this analysis for each participant separately. We defined a region of interest based on the peak coordinates for response errors (6, 51, 30) and response conflict (-6, 30, 39) in the pMPFC. We took the mean of both coordinates and drew a sphere of 15 mm around this centre. As a result, the region extended for the x-axis from -15 to +15, for the y-axis from 25 to 55 and for the z-axis from 20 to 50. Similar to the individual analyses on task and response errors we computed the percentage of brain activity uniquely related to response errors, uniquely related to response conflict and the percentage of overlapping activation. The threshold was set at $p < 0.05$ and no smoothing was applied. The overall percentage of overlap was minimal (1%). The largest percentage of overlap was 3%. Further, the percentage for response error and response conflict activity did not differ significantly, 53% and 46% respectively ($t(18) < 1$).

Second, we performed a conjunction analysis between the task error contrast and the task conflict contrast. As expected from the above task error contrast and task conflict contrast, the conjunction analysis showed no significant overlap. If we compare the regions associated with task conflict and task errors, we see that task conflict regions are located more posterior than task error regions.

See Figure 7 for an overview of the peak activations in the pMPFC for task errors, task conflict, response errors and response conflict.

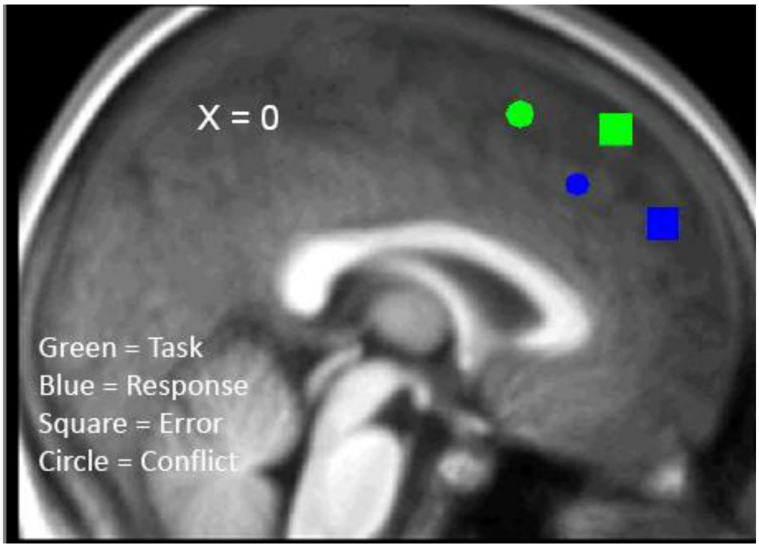

Figure 7. Peak activations in the pMPFC for task errors (MNI coordinates of maximal random-effect Z scores, x, y, z = 6, 39, 54, Z = 4.45), task conflict (MNI coordinates of maximal random-effect Z scores, x, y, z = -9, 15, 57, Z = 4.03), response errors (MNI coordinates of maximal random-effect Z scores, x, y, z = 6, 51, 30, Z = 3.87) and response conflict (MNI coordinates of maximal random-effect Z scores, x, y, z = -6, 30, 39, Z = 3.70). To represent all activations on the same figure all activations were mapped on an x-value of 0. Task related activation is presented in green and response related activation is presented in blue. Error related activation is presented as squares and conflict related activation is presented as circles.

GENERAL DISCUSSION

In this paper we investigated errors and conflict at two levels of abstractness. Our data show that task and response errors activate a region in the pMPFC that stretches from the rostral cingulate zone to the dorsal frontomedian cortex. A conjunction analysis on the group level revealed an overlap in brain activation for both types of errors. However, an investigation on the individual level did not support the conclusion of a strong overlap. Furthermore, the differential pattern of brain activation outside the pMPFC supports the hypothesis that task and response errors are related to different neural substrates. The second part of the analysis, comparing response and task conflict, also revealed a clear dissociation of the task and the response level. It seems that task conflict activates regions more posteriorly located than response conflict. However, it seems that both conflict types also share some overlapping activations outside the pMPFC such as the IFJ and the MFG. In the last part of the analysis we compared conflict and error processing within each level of abstractness. For both levels it seems that there is no overlap between conflict and errors. In addition, error activated regions seem to be located more anterior than conflict related regions. Further, this distinction is more salient at the task level than at the response level. A final point that supports the dissociation between the task and response level is provided by the behavioural data. It seems that participants are slower on task than on response errors ($p = 0.07$). In addition, response times are higher on task conflict than on response conflict trials. Even on subsequent trials the effect of task conflict is stronger than the effect of response conflict ($p = 0.06$), while it does not make a difference if a task error or a response error was made on the previous trial. In line with the fMRI data this shows that the difference between task and response processing is more expressed at the conflict level than at the error level.

DISSOCIATING TASK AND RESPONSE ERRORS

In the present study we found a distinction of task and response errors in the pMPFC. From the individual analysis it is clear that most participants do not show an overlap in response and task error activation. The question now is if we can dissociate both error regions anatomically. In accordance with our hypothesis, the data suggest that response errors rely on areas in the pMPFC that have a strong link to the motor system while task errors rely on areas in the pMPFC that are associated with more abstract processing. This dissociation is in accordance with the existing literature on task related and response related processes. As mentioned in the introduction response errors have been associated with ventral parts of the pMPFC, especially the RCZ (Ridderinkhof et al., 2004; Ullsperger & von Cramon, 2004). On the other hand in task related studies more dorsal regions such as the preSMA (Brass & von Cramon, 2002; Crone, Wendelken, Donohue, & Bunge, 2006; Rushworth, Hadland, Paus, & Sipila, 2002) seem to play an important role. The task error region that we described in the pMPFC (dFMC, dorsal frontomedian cortex) is more anterior to the preSMA and has been described in higher level decision processes. It seems that this region is involved under conditions were abstract rules have to be applied to a certain stimulus. For example, Volz and colleagues reported this region when participants where highly uncertain about their decisions compared to situations where participants could recollect their decisions from memory (Volz, Schubotz, & von Cramon, 2003; Volz, Schubotz, & von Cramon, 2004). Further, in a study of Goel and Dolan (2000) the dFMC was active if participants had to derive a classification rule themselves while there was no dFMC activity when participants had to classify stimuli based on predetermined features. In a similar experiment of Elliott and Dolan (1998) the dFMC was activated under situations of rule searching. Finally, Rushworth et al. (2002) reported the dFMC in situations where participants had to switch between different stimulus-response rules. In line with our results this suggests that the task error region is related to abstract processing. However, one should be cautious of the fact that activation in the dFMC was also found for response errors. Although this activation was not as strong as for task errors and was more posteriorly located, we cannot conclude that task errors exclusively activate dorsal regions and response errors exclusively activate ventral regions. However, we can conclude that both error types activate different subregions in the pMPFC.

From the individual analyses it seems that some participants show larger percentages for task errors while others show the opposite pattern. Such effects might be due to strategies in response selection. In previous research using univalent stimulus-response mappings it was shown that some participants first select the correct hand and then the correct finger while others first select the correct fingers (for example both middle fingers) and then the correct hand (Bernstein, Scheffers, & Coles, 1995). It was demonstrated that hand preference subjects (those who first select their hand) show larger error-related negativity to hand errors and vice versa. Mapped on our results this could explain why some participants have larger activation for task errors and others have larger activation for response errors in the individual analyses (if task errors are considered as hand errors and response errors as finger errors). However, unlike these previous studies, where only one task with four possible responses was offered, we offered two different tasks with each two possible responses. In addition, participants could already start preparing the task and the concurrent hand before information about the correct finger was forehand.

Further evidence for a differentiation between task and response errors is provided by the different brain networks both errors activate. Besides the prefrontal areas we found activation in the rMTG and the rINS for response errors and activation in the rIPL for task errors. The rMTG has been related to colour processing (Chao & Martin, 1999; Simmons, Ramjee, Beauchamp, McRae, Martin, & Barsalou, 2007). Presumably, this activation thus resulted from the changing colour situations in the stimulus change trials. The activation of the rINS on the other hand is probably related to the response switches made during stimulus change trials, as this region has been related to response switching (Paulus, Feinstein, Leland, & Simmons, 2005). As regards the rIPL activation, this region has been linked to the maintenance of current task goals and the processing of new task information (Singh-Curry & Husain, 2009). In the task error contrast two task switching situations were subtracted from one another. Thus, like

Singh-Curry and Husain (2009) we find support for the role of the IPL in flexible adaptive behaviour.

It should be mentioned that the response errors in our study were evoked in a different way than is usually done in the literature. Usually, response errors are elicited by the use of an interference paradigm such as the flanker task. However, in our study we wanted to elicit both errors in the same way so that the differences between them were kept as small as possible. Therefore response errors were also elicited by means of a stop change signal. One could argue that in this way we elicit another type of error than the response errors usually described. Further, the activation correlated with response errors was located more dorsal and more anterior in our study compared to the activation generally found for response errors. However, if we compared the response error activation in the pMPFC to the cluster of performance monitoring activation described by Ridderinkhof and colleagues (2004) our response error activation clusters were still situated in this zone. At first sight, the dFMC activation could be explained by the inhibition procedure we used. Similar dFMC activation was namely found in a stop signal study (Li, Huang, Constable, & Sinha, 2006). In a follow up study stopping was impaired when this region was disrupted by transcranial magnetic stimulation (Chen, Muggleton, Tzeng, Hung, & Juan, 2009). However, the fact that we found a distinction between the task and the response level shows that we do not merely assess inhibition processes but rather response and task related processes.

DISSOCIATING TASK AND RESPONSE CONFLICT

In addition to the error contrasts we performed conflict contrasts. Whereas response conflict activated the RCZ, the lIFJ, the rMFG and the lFMS, task conflict was associated with the preSMA, the PM, the lIFJ, the lDLPFC and the rMFG. The activation of the left frontopolar cortex in the response conflict contrast is probably related to the fact that we compared changing stimuli. Pollmann and colleagues already associated left frontopolar cortex with changes in visual dimension (Pollmann, 2000; Pollmann, Weidner, Muller, & von Cramon, 2000). The RCZ is often reported as a response conflict region, whereas task conflict seems to be correlated with regions associated with more abstract cognitive processes such as the preSMA and the premotor cortex (Abe, Hanakawa, Takayama, Kuroki, Ogawa, & Fukuyama, 2007). This anterior-posterior dissociation is partly reproduced in our response and task conflict related brain regions. However these effects should be treated with care since the conflict contrasts subtract two different trial types from each other. That is, we compared trials in which a secondary ellipse or stimulus is presented with trials where there are no secondary changes.

INTEGRATING 2 DIMENSIONS

Overall, we found that depending on the level at which an error occurs different brain regions are activated. This suggests that an error is more than a general comparison between an intended and an actual outcome. In addition, the dissociation in brain activity between different levels of errors could point to the difference in adjustments they apply for. The same conclusion can be formed based on our conflict results. Namely, different forms of conflict are correlated with different brain areas. This is in line with recent findings showing that the medial prefrontal cortex interacts with the lateral prefrontal cortex in a parallel hierarchical way to provide control (Kouneiher, Charron, & Koechlin, 2009).

Finally, we replicated the dissociation between conflict and errors at the response level. It seems that response errors activate regions more ventral and more anterior than response conflict areas. In addition, we found that conflict and errors were even more pronouncedly dissociated at the task level.

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CHAPTER 4
ERROR ADAPTATION IN MENTAL ARITHMETIC[1]

Until now, error and conflict adaptation have been studied extensively using simple laboratory tasks. A common finding is that responses slow down after errors. According to the conflict monitoring theory, performance should also improve after an error. However, this is usually not observed. In this study, we investigated if the characteristics of the experimental paradigms normally used could explain this absence. More precisely, these paradigms have in common that behavioural adaptation has little room to be expressed. We therefore studied error and conflict adaptation effects in a task that encounters the richness of everyday life's behavioural adaptation, namely mental arithmetic, where multiple solution strategies are available. In accordance with our hypothesis, we observed post-error accuracy increases after errors in mental arithmetic. No support for conflict adaptation in mental arithmetic was found. Implications for current theories of conflict and error monitoring are discussed.

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INTRODUCTION

Over the past decades, a lot of research has been conducted on how we adapt our behaviour following errors. A well replicated finding is that response times slow down after we encounter an error. This has served as evidence for adaptive control mechanisms taking place after an error. More specifically, an error is assumed to alter the point on the speed-accuracy trade off curve to a more conservative level, such that behaviour will be slower but more accurate (e.g., Brewer & Smith, 1984; Brewer & Smith, 1989, Rabbitt, 1979). These ideas have been integrated in current accounts of error monitoring. For example the *conflict monitoring account*, explains post-error slowing in terms of an increase in response thresholds after an error or conflict (Botvinick, Braver, Barch, Carter, & Cohen, 2001). According to these traditional accounts, response times will thus slow down and accuracy will increase after an error. Although post-error accuracy increases have been reported in some studies (e.g., Danielmeier, Eichele, Forstmann, Tittgemeyer, & Ullsperger, 2011; Laming, 1968; Marco-Pallares, Camara, Munte, & Rodriguez-Fornells, 2008; Seifert, von Cramon, Imperati, Tittgemeyer, & Ullsperger, 2011), other studies failed to find post-error accuracy increases (e.g., Hajcak, McDonald, & Simons, 2003, Hajcak & Simons, 2008; King, Korb, von Cramon, & Ullsperger, 2010; Notebaert & Verguts, 2011) or even observed post-error accuracy decreases (e.g., Fiehler, Ullsperger, & von Cramon, 2005; Rabbitt & Rodgers, 1977). This contradiction was addressed by Notebaert, Houtman, Van Opstal, Gevers, Fias and Verguts (2009). According to these authors, it is not the erroneous nature of the (incorrect) response but the fact that it occurs infrequently that explains post-error slowing. More precisely, an infrequent event attracts attention away from the task and in this way slows down subsequent processing. Notebaert and colleagues (2009) confirmed this hypothesis by showing post-error slowing after infrequent errors, but post-*correct* slowing after infrequent *correct* responses. In addition, they showed that irrelevant and infrequent sounds also slowed down performance on subsequent trials. In sum, according to these authors, post-error slowing should be considered as an attentional effect (or an orienting response) rather than as an adaptation effect. In contrast to the conflict monitoring account, these authors do not predict post-error accuracy increases but rather post-error accuracy *decreases*. Indeed, because infrequent events such as errors capture attention, task processing will be impaired, resulting in post-error accuracy decreases.

In the laboratory, error monitoring has been studied extensively with a wide range of tasks. Typically, in these tasks, different stimuli are mapped in an arbitrary way onto different responses. For example, a red square has to be responded with a left button and a green square with a right button. To fulfill such a task it is important to notice the difference between the stimuli, to remember the stimulus-response mappings and to push the according button appropriately. Thus, correct task performance in these tasks, comprises a correct identification of the stimulus and the selection and execution of the corresponding button. In the remaining part of the manuscript we will refer to these tasks as direct mapping tasks.

However, in daily life, appropriate behaviour is not only determined by a simple stimulus. Often, more complex cognitive processes are required, e.g., when multiple solution strategies are possible. For example when a traffic light suddenly turns orange, you can choose between stopping or driving through. However, the behaviour that will eventually be chosen will not only depend on the stimulus (the orange light) but also on other factors; the police car next to you, the fact that you are already late for an appointment, your driving speed,... It is clear that, depending on the situation, some strategies are more efficient than others. So in contrast to direct mapping tasks, the stimulus identification in itself is not enough to elicit the most efficient behaviour. In parallel, error adaptation in direct mapping tasks will be restricted to specific strategies, namely paying more attention to the relevant stimulus and refreshing the appropriate stimulus-response mappings. For example, consider a task where participants should respond with a left button to the digit 3 and with a right button to the digit 8. When the digit 3 is categorized incorrectly with the right button, the only possible strategy to prevent this error in the future, is to pay more attention to the presented digit and to recall the rule: 3-left, 8-right. In a way, there is thus not much to do after an error has been made, except for looking more attentively to the screen and to remember the response rules. Therefore, post-error effects, measured in direct mapping tasks might indeed only reflect an orienting response (as suggested by Notebaert et al., 2009). However, error adaptation in more complex situations should not be restricted to an attention increase or rule refreshment and might therefore elicit, besides an orientation response, also an improvement in behaviour (post-error accuracy increase). Unfortunately, such more complex tasks have largely been neglected in classical error monitoring research. In this paper we will fill this gap and investigate error adaptation effects in a more complex and daily used task that involves more cognitive processes and permits a selection between different strategies, namely mental arithmetic. Participants were asked to verify simple multiplication problems (e.g., 4 x 6 = 24 correct / false?). Different strategies have been documented in the verification of multiplications. Besides retrieving the answer from memory and comparing the retrieved answer to the presented one, participants can also use different rules to verify the presented solutions. For example, the ‘five rule’ comprises that when one of the operands is 5, the product should have 0 or 5 as a final digit (Campbell & Graham, 1985; Siegler, 1988). Another example is the ‘parity rule’, which states that if at least one of the operands is even, the outcome must also be even (Krueger, 1986; Lemaire & Fayol, 1995; Lemaire & Reder, 1999; Masse & Lemaire, 2001). (For other examples of strategies in arithmetic verification see Ashcraft & Stazyk, 1981; Winkelman & Schmidt, 1974; Zbrodoff & Logan, 1986).

The advantage of using multiplication verification (and not production or another operation, like addition) is that we can manipulate the table relatedness of the presented distracters. As we know from previous studies, it is more difficult to reject a closely related distracter (e.g., 4 x 6 = 28) compared to an unrelated distracter (e.g., 4 x 6 = 14) (Campbell, 1987; Stazyk, Ashcraft, & Hamann, 1982). The idea of a multiplication 'network' in which activation spreading is at work, is now generally accepted (Ashcraft, 1987; Campbell, 1995; McCloskey & Lindemann, 1992; Verguts & Fias, 2005) and explains the influence of table relatedness in a verification task. Hence, in the present study we defined 'conflict' in terms of table relatedness: 4 x 6 = 14 is a low conflict trial since 14 is not related to the table of 4 nor to the table of 6. On the other hand, 4 x 6 = 28 is a high conflict trial since 28 belongs to the table of 4 (4 x 7). Further, our high conflict trials were always one step away from the correct outcome (4 x (6+1) = 28) to maximize the amount of conflict (further called 'distance 1 distracters'). In this study, conflict is thus defined as the distance between the correct answer and the presented answer. Consequently, conflict is not defined at a response level or at a stimulus level, as is the case in most laboratory tasks, but at a higher cognitive level.

A robust finding in the cognitive control literature is the fact that interference effects (the difference between high and low conflict trials) are smaller after conflicting stimuli. This effect was initially demonstrated by Gratton, Coles and Donchin (1992) in the flanker task and has now been observed in a wide range of tasks (Simon tasks: Sturmer, Leuthold, Soetens, Schroter, & Sommer, 2002, Stroop tasks: Kerns, Cohen, MacDonald, Cho, Stenger, & Carter, 2004, and prime-target congruency effects: Kunde, 2003). The logic behind this observation is that conflict trials call for more control and therefore cause benefits on subsequent trials. A recent model for conflict adaptation by Verguts and Notebaert (2009) explains conflict adaptation by a strengthening of S-R associations (e.g., target arrow pointing leftwards means left response) at the moment conflict is detected. The crucial aspect of this Hebbian-like model is that only associations that are active at the time conflict is detected, will be strengthened. In mental arithmetic, there is support that "4 x 6" will activate certain table related solutions (Campbell, 1987; Stazyk et al., 1982) but given the large amount of arithmetic problems and solutions, it is unlikely that performance on the immediately subsequent trial will benefit from this strengthened activation. In other words, what is the advantage of strengthening “4 x 6 = 24”, if on the next trial “5 x 3 = 18” is presented? Consequently, no conflict adaptation effects are expected.

In sum, conflict and error monitoring theories are based on studies using direct mapping tasks, in which paying more attention to the crucial stimulus and refreshing the stimulus-response rules are the only way in which performance can be increased. Although post-error effects have been depicted as markers of adaptive behaviour, not all data are in line with this hypothesis (i.e., the absence of post-error accuracy increases). Recent accounts even question the adaptive nature attributed to post-error effects (Notebaert et al., 2009). However, we believe that the use of more complex tasks (i.e., in which multiple solution strategies are possible) might provide additional information to this debate. More precisely, because behavioural adaptation is very limited in direct mapping tasks, post-error effects in these tasks might predominantly reflect an orienting response. However, in more complex everyday tasks, behaviour can be adapted in a countless number of ways. In other words, there is more room to improve subsequent behaviour. One of the tasks where we expect post-error adjustments to be more than a generic slowing down is mental arithmetic. After an error in this task, participants have the opportunity to change strategies in order to improve performance. Subsequently, we expect post-error accuracy increases in addition to post-error slowing in mental arithmetic. Finally, due to the large amount of different stimuli and responses in our task, we predict no conflict adaptation in mental arithmetic.

METHOD

PARTICIPANTS

35 students at Ghent University (16 females) participated in this study (mean age = 19.3 years, SD = 1.2 years). The majority of the

participants earned course credits in exchange for participation. The other participants were paid 8 euro.

MATERIAL

Stimuli were presented on a 17-inch computer screen. The viewing distance was about 50 cm. The multiplication problems were centered on the screen in the traditional format (e.g., 3 x 7 = 21) and presented in white on a black background (total outline: 4.2 cm x 0.6 cm). Responses were recorded by response boxes. The experiment was conducted using Tscope software (Stevens, Lammertyn, Verbruggen, & Vandierendonck, 2006).

STIMULI

Three different types of multiplication problems were presented. Half the trials comprised problems presented with a correct solution (CORRECT: 4 x 6 = 24). The other half of the trials comprised problems presented with an incorrect solution (distracters). For the incorrect solutions, we manipulated the distance from the correct solution in the multiplication network. More precisely, in one fourth of the trials the distracter was one step away from the correct solution (DISTANCE 1: 4 x 6 = 28), whereas in the other fourth of the trials the distracter was unrelated to the correct solution (UNRELATED: 4 x 6 = 21). Transitions between these different trial types were pseudo-randomized over the experiment, in such a way that every possible transition occurred equally often. We selected problems ranging from 2 x 3 until 8 x 9. Tie problems were not included. This resulted in 28 problems. For unrelated distracters one unrelated outcome was chosen for each of the 28 problems. Every problem occurred in both the ‘larger x smaller’ and the ‘smaller x larger’ order. This resulted in 56 unique problems for correct and unrelated problem types. For correct problems, these 56 problems were repeated 8 times over the experiment, for unrelated problems they were repeated 4 times. For distance 1 distracters we included four different outcomes for each of the 28 problems: (a+1) x b; (a-1) x b; a x (b+1); a x (b-1). For distance 1 distracters, there were thus four lists of 28 problems[2]. Including the order of larger operand first /smaller operand first, there were 224 problems for distance 1 distracters. Every problem was repeated once during the experiment. In practice the four different distance 1 lists sometimes contained the same distracters. This was the case for problems with 2 or 9 as one of the operands (e.g., 2 x 7 or 9 x 3) because problems with 1 (e.g., (2-1) x 7) or 10 as one of the operands (e.g., (9+1) x 3) were excluded from the stimulus set. In total, there were 896 experimental trials.

A number of restrictions were imposed on the stimuli. First of all, we ensured that the ‘split’ (i.e., the magnitude difference between the presented distracter and the correct product, Ashcraft & Stazyk, 1981; Koshmider & Ashcraft, 1991) did not differ significantly between distance 1 distracters (mean split = 5.5) and unrelated distracters (*M* = 4.5), *t*(27) = 1.42, *p* =.17. Second, the direction of the split was controlled: half of the distracters was larger than the correct product, the other half was smaller than the correct product, for both distracter types. Third, the magnitude of the presented distracters did not differ significantly between distance 1 (*M* = 29.63) and unrelated distracters (*M* = 28.39), *t*(27) = 1.23, *p* =.23.

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[2] Because there were four possible distance-1 solutions per problem and only one possible unrelated solution per problem, we repeated all analyses restricted to the data gathered in the first block, thus only including the first presentation of both solution types. All results were replicated, indicating that the different presentation frequency of high and low conflict was not responsible for the pattern of results.

PROCEDURE

Participants had to classify multiplication problems as correct or incorrect by pressing a button with their left or right index finger. The response mappings were counterbalanced between subjects.

In total there were four blocks of 226 trials resulting in 904 experimental trials. The experiment started with 8 practice trials. There was a short break after every block. During the break the mean reaction time of the participant appeared on the screen. The experiment lasted about 40 minutes. Participants were instructed to respond both fast and accurately.

Each trial started with the presentation of the following fixation mark '!' for 500 ms. Then the verification problem appeared on the screen until participants responded or until the response deadline of 1500 ms had passed. After a correct response, a green circle was presented for 500 ms while after an erroneous response a red circle appeared. If participants did not answer within the response interval the words 'TE TRAAG' (too slow) appeared on the screen for 500 ms. After a blank screen of 300 ms the following trial started, resulting in a response stimulus interval of 1300 ms.

RESULTS

Three participants were removed from the analyses. The error rates of two participants were larger than 2 SD's from the overall mean. The data of the third outlier indicated guessing behaviour, shown by a lot of (23%) very fast (< 200 ms) responses. The mean response time of the remaining 32 participants was 832 ms (SD = 93 ms). The mean error rate was 14% (SD = 5%). Correct trials (in which a problem was presented with its correct product) were not included in the analyses since they only served as control trials. In the final dataset we thus only included unrelated and distance 1 trials. Furthermore, responses exceeding the response deadline were discarded (3%, SD = 4%). We also excluded responses following these trials (3%, SD = 4%). In addition, errors on the current trial (17%, SD = 8%) were removed for response time analyses. For each dependent variable (RTs and accuracy) we first compared post-correct performance with post-error performance by means of a paired samples *t*-test. Second, we looked at conflict adaptation effects by means of a 2 x 2 repeated measures ANOVA on post-correct trials including the factors INTERFERENCE N-1 (trial n-1 unrelated versus trial n-1 distance 1) and INTERFERENCE (unrelated versus distance 1). In the first section, we report the results for response times. In the second section, the results for accuracy rates are described.

RESPONSE TIMES

Response times for error trials (882 ms, SD = 114 ms) were significantly slower than for correct trials (855 ms, SD = 98 ms), $t(31) = 2.52$, $p < 0.05$. Participants responded slower after an error (951 ms, SD = 93 ms) than after a correct response (874 ms, SD = 103 ms), $t(31) = -6.37$, $p < 0.001$. See Figure 1. Further, the expected interference effect emerged. Participants were slower on distance 1 trials (897 ms, SD = 107 ms) than on unrelated trials (851 ms, SD = 105 ms), $F(1,31) = 81.44$, $p < 0.001$. However, the main effect of INTERFERENCE N-1 and the interaction between INTERFERENCE N-1 and INTERFERENCE did not reach significance, *Fs* < 1. Mean response times are shown in Table 1.

ACCURACY

Participants were more accurate after an error (84%, SD = 8%) than after a correct response (81%, SD = 8%), $t(31) = -2.86$, $p = 0.01$, see Figure 1.

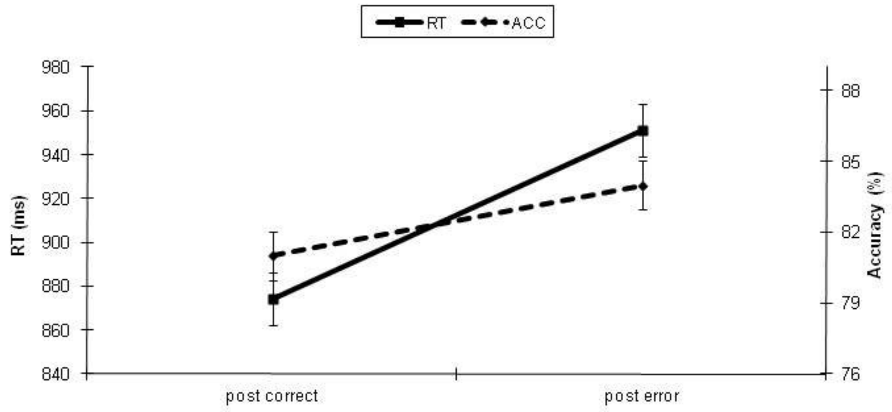

Figure 1. Mean response times (in ms) and accuracy rates (in percentage) on trials following a correct response (post-correct) or an error (post-error).

Further, participants were less accurate on distance 1 trials (75%, SD = 10%) than on unrelated trials (87%, SD = 8%), $F(1,31) = 125.74$, $p < 0.001$. There was no main effect of INTERFERENCE N-1, $F < 1$. The interaction between INTERFERENCE N-1 and INTERFERENCE was significant, $F(1,31) = 8.71$, $p = 0.01$. However, the results do not support reduction of interference after high conflict. Rather they point into the opposite direction: there is more interference after distance 1 trials than after unrelated trials. Mean accuracy rates are shown in Table 1.

Table 1. Mean response times in ms and accuracy rates (between brackets) in percentages, for previous trial type (unrelated and distance 1) and current trial type (unrelated and distance 1).

		Current trial	
		Unrelated	Distance 1
Previous trial			
	Unrelated	851 (0.86)	894 (0.76)
	Distance 1	850 (0.89)	900 (0.74)

GENERAL DISCUSSION

The simplified nature of laboratory tasks might have narrowed the perspective on error monitoring. Moreover, post-error accuracy increases are not always observed in direct mapping tasks. As a result, post-error effects in these tasks (i.e., post-error slowing) have been explained by attentional effects (i.e., orienting to the error, attracting attention away from the task) rather than by adaptation effects. Our data suggest that in a more complex task, i.e., tasks where multiple solution strategies are possible and where people can adjust their behaviour by flexibly switching between these strategies, attentional effects are not sufficient to explain the data pattern. In sum, post-error adaptation effects (such as post-error accuracy increases) might predominantly be observed in more complex tasks, as shown in the present study.

The difference in complexity between our task and direct mapping tasks is also expressed in the response times on errors. Namely, we found larger response times on errors compared to correct responses in mental arithmetic. In direct mapping tasks, where one strategy (i.e., paying more attention to the stimulus and refreshing the stimulus-response rules) is the only way to improve performance, an error will primarily result from insufficient processing time. Errors in direct mapping tasks thus typically emerge on fast trials. However, in tasks that do not only rely on stimulus identification, errors will primarily occur on difficult trials (i.e., multiplication problems where the correct solution is not that straightforward) compared to trials where participants can immediately recollect the correct solution from memory. Consequently, over the whole experiment errors will be slower than correct responses.

Further, to investigate conflict adaptation, we manipulated the relatedness of the distracters: distance 1 distracters were responded slower and less accurate than unrelated distracters. However, reduction of interference after high conflict was not observed. This indicates that conflict adaptation, a process at work in direct mapping tasks, might not be at work in more complex tasks. In the introduction we argued that on the basis of associative control models (Verguts & Notebaert, 2009), one would not predict conflict adaptation in mental arithmetic, or any other task consisting of multiple stimuli and responses (e.g., Braem, Verguts & Notebaert, 2011). This is in line with our findings. On accuracy rates, the results even pointed into the opposite direction. Interference was *reduced* after unrelated trials compared to distance 1 trials. At first sight these results might seem odd. However, in a recent ERP-study, Tzur and Berger (2007) showed that theta activity, a measure expressing anterior cingulate cortex activity in error and conflict detection (Luu, Tucker, & Makeig, 2004), is related to the salience of the rule violation in mental arithmetic. More precisely, a larger deviation from the correct response was related to more theta activity. In our experiment, unrelated distracters were more salient violations from the correct response than were distance 1 distracters. That is, distance 1 distracters are still related to the multiplication table of one of the operands, whereas unrelated distracters are not related to the operands. In other words, salience and conflict are not confounded in our design. In contrast, in direct mapping tasks high conflict trials are often also the most salient trials. Our results thus might suggest that interference effects are reduced after more salient events. This implicates that not the level of conflict but rather the salience of the event is important to reduce interference effects. Of course, future research is necessary to investigate this possibility.

Taken together, the present study shows that it is crucial to investigate error processing and conflict adaptation in tasks that resemble daily situations of flexible behaviour. Not all effects found in direct mapping tasks can be generalized to more complex tasks. We are convinced that broadening the domain by extending the sort of tasks being used, will gain new and interesting insights in the human ability of cognitive control, decision making, and flexible behaviour.

Besides the broader view on cognitive control processes our study provides some important implications for research in mental arithmetic. Traditionally, researchers in this domain focus on RTs of correct responses and on percentages of errors (e.g., Campbell & Xue, 2001; Imbo & Vandierendonck, 2007a,b; LeFevre, Bisanz, Daley, Buffone, Greenham, & Sadesky, 1996; Seitz & Schumann-Hengsteler, 2000; Siegler & Lemaire, 1997; Smith-Chant & LeFevre, 2003; etc.). Mostly, response times after errors are not discarded from the analyses. Nonetheless, errors are not that infrequent in mental arithmetic. For example, in a multiplication production task under time pressure, adults make between 1% and 35% errors (De Brauwer, Verguts & Fias, 2006; Imbo & Vandierendonck, 2010; Smith-Chant & LeFevre, 2003; Verguts & Fias, 2005). Future studies in the field of mental arithmetic need to be aware of post-error effects. More specifically, we would suggest removing not only error trials but also trials that follow errors.

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CHAPTER 5

WHEN THE COFFEE MACHINE IS WRONG: THE ROLE OF THE MEDIAL PREFRONTAL CORTEX IN ERROR OBSERVATION[1]

Recent research suggests that similar brain areas in the posterior medial prefrontal cortex (pMPFC) are active when we make errors ourselves and when we observe erroneous behaviour of other people. This has led to the conclusion that monitoring errors of other people might be achieved by motor simulation of these errors. This raises the fundamental question how we are able to detect errors of machines, that we cannot simulate in our motor system? Here we show that observing machine errors activates the same region in pMPFC than observing human errors, indicating that medial prefrontal brain circuits are not only dedicated to monitor human errors. Furthermore, our findings suggest that the crucial mechanism involved in error monitoring is based on indentifying violations of expectancies. These findings have far reaching implications for our understanding of how we identify erroneous events in the environment. Our data suggest that a domain general mechanism of monitoring violations of expectancies allows us to identify errors in humans and machines.

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[1] This manuscript has been submitted for publication and is co-authored by Eliane Deschrijver and Marcel Brass

INTRODUCTION

Detecting errors is extremely crucial to adapt our behaviour to the environment. We learn from our own and other people's errors. Given the importance of being able to detect errors, it is not surprising that there is a brain system in the posterior medial prefrontal cortex (pMPFC) dedicated to this function (Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004; Ullsperger & von Cramon, 2004). Interestingly, pMPFC is also activated when we observe other humans making errors (de Bruijn, de Lange, von Cramon, & Ullsperger, 2009; Manthey, Schubotz, & von Cramon, 2003; Newman-Norlund, Ganesh, van Schie, de Bruijn, & Bekkering, 2009; Shane, Stevens, Harenski, & Kiehl, 2008). This shared brain activity during error observation and error execution has been suggested to reflect an internal simulation of an observed error (e.g., Bates, Patel, & Liddle, 2005; Bekkering, de Bruijn, Cuijpers, Newman-Norlund, van Schie, & Meulenbroek, 2009; van Schie, Mars, Coles, & Bekkering, 2004). But what happens if we observe errors that we cannot simulate such as errors of machines? Do such errors also active pMPFC? In the current functional magnetic resonance imaging (fMRI) study we investigated this question by contrasting brain activity related to the observation of errors than can be simulated with brain activity related to the observation of errors that cannot be simulated. More precisely, we used functional brain imaging while participants observed daily life human-machine interactions that resulted in correct or erroneous situations. The reason for these errors could be twofold. First, the human caused the error by incorrectly operating the machine (human error). Second, the error could be caused by a malfunctioning of the machine (machine error). If pMPFC is uniquely activated during the observation of human errors, this would lend further support to the simulation hypothesis. On the other hand, if we find pMPFC in both conditions, the role of this brain area in error observation has to be considered more general.

METHOD

PARTICIPANTS

Twenty-three participants (19 females) participated in the experiment (mean age = 21.3 years, SD = 2.2 years). All participants were paid 25 euro for their participation. They were all right handed as was measured by the Edinburgh Inventory (Oldfield, 1971). All participants gave written informed consent and had no history of neurological disorders. Ethical approval was given by the Medical Ethical Review Board of the Ghent University hospital.

STIMULI AND DESIGN

The experiment was implemented using Presentation software (Neurobehavioral Systems, Albany, NY, USA). Every trial consisted of a short movie, showing a daily situation of a human-machine interaction. Eight different situations were presented in the study (coffee machine, elevator, photocamera, electronic garage door, semi-automatic doors, vending machine, photocopier and digital clock). According to the characteristics of the human-machine interaction, three conditions were specified. First, the person could perform a correct action after which the machine would produce the correct outcome (CORRECT). For example, in the coffee machine situation the person would press the correct button on the machine after which the machine would pour the coffee correctly into the cup. Second, the person could perform an incorrect action resulting in an incorrect outcome (HUMAN ERROR). In the example of the coffee machine, the person would press the button corresponding to two cups of coffee. As a result, too much coffee is being poured into the cup and the coffee is spilled. Third, the person could perform a correct action, leading however to an incorrect outcome produced by the machine (MACHINE ERROR). Considering the above- mentioned example, the person would press the button for one cup of coffee, but nevertheless too much coffee is poured into the cup and again the coffee is spilled.

Human errors become apparent from the moment the person performs the incorrect action. The erroneous result of this action will thus be expected. Machine errors on the other hand, are not caused by an incorrect human action. Therefore, these errors are not expected in the series of ongoing events. An additional difference between human errors and machine errors is thus the predictability of the erroneous outcome. However, because this problem is inherent to the characteristics of the errors (namely; a machine error will always be unexpected, whereas a human error is the results of an incorrect action) we controlled for this issue by including an extra condition in which the correct action and outcome were presented but where an unexpected object, unrelated to the situation, appeared on the screen (EXPECTATION). In the above example, this would mean that there is an unrelated picture (for example a chair) presented in one of the quadrants of the screen at the moment the coffee is poured into the cup. Eight different objects were used in the 8 different situations. Furthermore, over the whole experiment, the objects were presented equally often in each quadrant of the computer screen. The picture remained on the screen until the movie ended. If a difference in brain activity between human errors and machine errors can be explained by the unexpected nature of a machine error, we should also find this activity in the expectation condition.

In total, there were 32 unique trials (8 situations x 4 conditions). These trials were repeated three times resulting in 96 experimental trials. The duration of each movie was dependent on the situation and the condition (mean duration = 28.22 sec, SD = 9.50 sec). However, for each situation we constructed a video clip that was very similar for the four conditions (correct, human error, machine error and expectation). Only the crucial event was changed (for example the moment of the action). In this way, the movies belonging to the different conditions were kept as equal as possible. To make sure participants paid attention to the videos, we sometimes asked a question about the previously presented video clip. Over the whole experiment, 8 questions were asked. These questions were divided over the 8 different situations and over the 4 conditions. The question always resulted in a multiple choice answer with 4 possibilities. The questions were presented in white on a black background. The trials preceding a question were discarded from the analysis, resulting in 88 experimental trials.

PROCEDURE

Participants were lying in the scanner while they attentively watched the movies. Each trial started with the presentation of a fixation cross for 200 ms, after which the movie started. The intertrial interval was varied in a pseudo logarithmic fashion. Using steps of 300 ms, 50% of the trials used a jitter ranging from 200 to 1100 ms, 30% of the trials used a jitter ranging from 1400 to 2300 ms and 20% of the trials used a jitter ranging from 2600 to 3500. The mean interval was 1250 ms. When a question was presented on the screen, participants had to respond by means of two response boxes that were placed on their upper legs. Responses were given with the index and middle fingers of each hand. The mapping of the responses to the different answers of the multiple choice question was indicated on the screen. A short break was inserted in the middle of the experiment.

FMRI METHODS

The experiment was carried out on a 3T scanner (Siemens Trio) using an 8-channel radiofrequency head coil. Subjects were positioned head first and supine in the magnet bore. First, 176 high-resolution anatomical images were acquired using a T1-weighted 3D MPRAGE sequence (TR = 2530 ms, TE = 2.58 ms, image matrix = 256 ×256, FOV = 220 mm, flip angle = 7º, slice thickness = 0.90 mm, voxel size = 0.9 ×0.86 × 0.86 mm (resized to 1×1×1 mm)). Whole brain functional images were collected using a T2*-weighted EPI sequence, sensitive to BOLD contrast (TR = 2000 ms, TE =35 ms, image matrix = 64 × 64, FOV = 224 mm, flip angle = 80º, slice thickness = 3.0 mm, distance factor = 17%, voxel size 3.5 × 3.5 × 3 mm, 30 axial slices). All data were analyzed using SPM5 (http://www.fil.ion.ucl.ac.uk/spm/software/spm5/). To account for T1 relaxation effects each EPI sequence started with two dummy scans. First, all functional images were spatially realigned using rigid body transformation. After the realignment the images were slice time corrected using the first slice as a reference. The structural image of each subject was co-registered with their mean functional image. Further, all functional images were normalized to the Montreal Neurological Institute (Montreal, Quebec, Canada) T1 template. The images were resampled into 3.5 mm^3 voxels and spatially smoothed with a Gaussian kernel of 8 mm (full-width at half maximum). A high pass filter of 128 seconds was applied during fMRI data analysis. Statistical analyses were performed using the general linear model implemented in SPM5. We distinguished correct trials, human error trials, machine error trials and expectation trials. Because human errors are defined at the moment of the action (the moment the button is pressed in the coffee machine situation) and machine errors at the moment of the outcome (the moment the coffee is spilled in the coffee machine situation) we defined both moments as separate regressors in the GLM, resulting in 8 regressors (4 conditions x 2 moments). When comparing different conditions in the whole brain contrasts, both moments (moment of the action and moment of the outcome) of one condition were always compared to both moments of the other condition. Both a canonical hemodynamic response function (HRF) and the first time derivative were modeled on these moments. We computed contrast images by comparing the parameter estimates for the regressors containing the canonical HRF. To account for residual movement effects, six regressors defining head movement were included in the model. A familywise error correction (FWE) was used with $p < 0.05$. All clusters containing more than 5 voxels were reported in the results section. First, we will describe three whole brain contrasts revealing activation related to human errors, machine errors and the occurrence of unexpected events respectively. Second, we performed a conjunction analysis on these three whole brain contrasts. This conjunction analysis reveals which brain areas are commonly activated by the three selected brain contrasts applying a FWE correction with a threshold of $p < 0.05$. Finally, we computed percent signal-change analyses. These were carried out using the MARSBAR toolbox constructed for SPM5 (Brett, Anton, Valabregue, & Poline, 2002). Based on the conjunction analysis, we extracted a region of interest with the following peak coordinate (6 24 57). In this ROI, a sphere was drawn with a 6-mm diameter around the peak coordinate.

RESULTS

We computed whole-brain contrasts to examine brain activation related to human errors, machine errors and the occurrence of unexpected events. To this aim, we subtracted brain activity in the correct condition from that in the human error condition, the machine error condition and the expectation condition respectively. The main focus of our analysis was the pMPFC (for a complete list of activations, see Table 1). As expected, brain activation related to human errors was found in the pMPFC. In particular, the activation was located in the presupplementary motor area (preSMA, BA8). Very similar pMPFC activation was registered after the subtraction of correct situations from machine error situations. As in the first contrast, the activation peak was located in the preSMA (BA8). Interestingly, the third contrast (subtracting correct situations from unexpected events) also revealed pMPFC activation. Here, the activation cluster was even more extended than in the previously described contrasts. More precisely, a region stretching from the supplementary motor area (SMA, BA 6), over the preSMA (BA 8) into the rostral cingulate zone (RCZ, BA 32) was revealed. The conclusions based on these results are twofold. First, the data suggest that the activation in the pMPFC is not specific for the observation of human errors. Second, the pMPFC activation is not uniquely related to the observations of errors but rather to the observation of a surprising or unexpected event. To further investigate this last matter, we performed a signal change analysis in the part of the pMPFC where the three previously described contrasts showed an overlap in activation. This overlap was defined by computing a conjunction analysis on all three contrasts (peak coordinate = 6 24 57, z = 4.98, extend = 6). If activation in the pMPFC is related to violations in expectancy, we should find the largest percent signal change during the observation of machine errors and non-erroneous unexpected stimuli. Further, for human errors, the percent signal change should not be higher at the moment the human error is perceived compared to the moment of the human action, because the human error can already be expected based on the previously executed action. A repeated-measures ANOVA analysis with the factors CONDITION (correct, machine error, human error and expectation) and MOMENT (moment of the action and moment of the outcome) was conducted on the percent signal change in the overlapping region. The analysis revealed significant main effects of CONDITION ($F(3,54) = 19.42$, $p < 0.001$) and MOMENT ($F(1,18) = 72.48$, $p < 0.001$). Furthermore, the interaction between both factors reached significance, $F(3,54) = 18.98$, $p < 0.001$. Paired comparisons showed that for machine errors and the expectation condition, the percent signal change at the moment of the outcome was substantially larger than at the moment of the action (machine errors: $F(1,18) = 58.50$, $p < 0.001$; expectation: $F(1,18) = 35.62$, $p < 0.001$). Moreover, these signal changes were larger than the percent signal change at the moment of the outcome for human errors, $F(1,18) = 86.88$, $p < 0.001$. Further, there was no difference in the percent signal change related to human errors for both moments ($F(1,18) = 2.09$, $p = 0.17$). Thus in line with what we hypothesized above, the percent signal change in the pMPFC coincides with the unexpectedness of the event (see Figure 1). More precisely, the events that are the most unexpected showed the largest percent signal change.

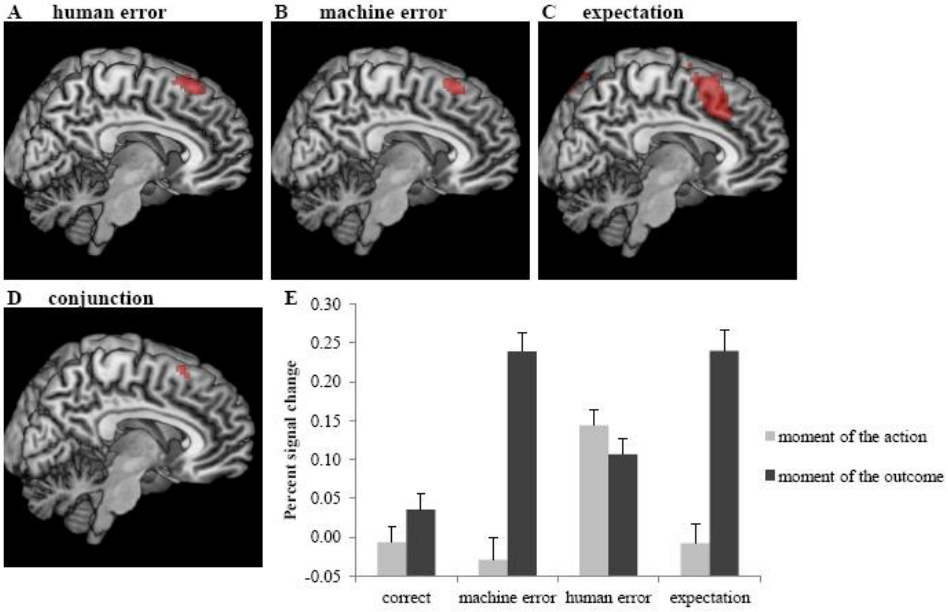

Figure 1. Results of the fMRI analyses. **A**, Sagittal view of pMPFC activity related to the contrast human errors – correct, MNI peak coordinate: 6 30 57. **B**, Sagittal view of pMPFC activity related to the contrast machine errors – correct, MNI peak coordinate: 6 24 57. **C**, Sagittal view of pMPFC acitivity related to the contrast expectation – correct, MNI peak coordinate: -3 18 48. **D**, Brain activity related to the conjunction analysis performed on the contrasts specified in A, B and C (A ∩ B ∩ C), MNI peak coordinate: 6 24 57. **E**, Percent signal changes for the area obtained in the conjunction analysis (MNI peak coordinate: 6 24 57) for the correct, the human error, the machine error and the expectation condition at the moment of the action and the moment of the outcome.

Finally, we wanted to investigate whether there were other brain regions that distinguish between the observation of human errors and the observation of machine errors. Therefore, we directly subtracted the brain activation related to the human error condition from the brain activation related to the machine error condition and vice versa. We found stronger activation for human than machine errors in the right and left premotor cortex (rPM, lPM), superior parietal lobe (SPL), inferior parietal lobe (IPL), and activation in the left and right middle temporal gyrus (MTG). These latter clusters extended into the lateral occipitotemporal cortex and comprised the extrastriate body area (EBA) and the human MT+ complex (MT+) (Downing, Peelen, Wiggett, & Tew, 2006; Weiner & Grill-Spector, 2011). For a complete list of activation related to the human error – machine error contrast see Table 1. On the other hand contrasting machine errors with human errors did not reveal any significant activation.

Table 1. MNI Coordinates of Whole Brain Contrasts

	Peak coordinates	Z-score	Cluster size
Human error (human error – correct)			
pMPFC (preSMA, BA8)	6 30 57	6.24	60
Inferior frontal gyrus	54 30 0	6.68	239
Inferior frontal gyrus	-60 18 15	5.45	53
Precentral gyrus (PM)	30 -9 57	4.85	7
Inferior parietal lobe	-42 -42 51	7.01	246
Inferior parietal lobe	60 -48 39	5.49	126
Inferior parietal lobe	-60 -51 36	5.10	36
Middle temporal gyrus	54 -66 6	6.18	267
Middle temporal gyrus	-57 -57 6	5.77	219
Machine error (machine error – correct)			
pMPFC (preSMA, BA 8)	6 24 57	5.51	26
Inferior frontal gyrus - anterior insula	54 21 9	5.93	126
Inferior frontal gyrus	-54 21 12	4.88	13
Anterior insula	-33 24 0	4.86	7
Middle temporal gyrus	-57 -57 6	5.28	46

Expectation (expectation – correct)			
pMPFC (preSMA + RCZ) + SMA	-3 18 48	6.27	428
Inferior frontal gyrus - anterior insula	-51 15 -3	5.98	150
Inferior frontal gyrus - anterior insula	45 18 3	5.66	142
Inferior frontal sulcus	-45 6 39	5.89	136
Middle frontal gyrus	-39 57 12	5.31	36
Middle frontal gyrus	27 63 24	4.93	21
Inferior parietal lobe	-33 -60 51	6.04	289
Inferior parietal lobe	33 -60 51	5.16	38
Precuneus	18 -78 48	4.73	5
Fusiform gyrus	33 -51 -12	6.08	66
Middle temporal gyrus	-60 -54 15	5.77	70
Middle occipital gyrus	39 -84 15	5.17	50
Middle occipital gyrus	-33 -90 9	5.14	19
Human versus Machine (human error-machine error)			
Precentral gyrus (PM)	24 -6 57	5.50	55
Precentral gyrus (PM)	-21 -9 60	5.63	49
Inferior parietal lobe	-36 -36 45	6.21	211
Superior parietal lobe	15 -54 66	5.35	26
Middle temporal gyrus	54 -69 9	5.21	40
Middle temporal gyrus	-42 -75 9	6.82	160

GENERAL DISCUSSION

The pMPFC has been primarily known as a region involved in performance monitoring. More precisely, numerous studies have related pMPFC activity to the occurrence of conflict, the commission of own errors and decision uncertainty (for reviews see Ullsperger & von Cramon, 2004; Ridderinkhof et al., 2004). However, recent studies have shown consistent pMPFC activation related to error observation as well (de Bruijn et al., 2009; Manthey et al., 2003; Newman-Norlund et al., 2009; Shane et al., 2008). As such, the execution and observation of errors seem to activate the same brain circuits. Similarly, in the domain of action understanding shared brain mechanisms for observation and execution have been well documented. Consequently, it has been hypothesized that we understand each other's actions by means of internal motor simulation (Iacoboni, Molnar-Szakacs, Gallese, Buccino, Mazziotta, & Rizzolatti, 2005; Rizzolatti & Craighero, 2004; Rizzolatti, Fogassi, & Gallese, 2001). Because error execution and error observation also rely on a similar brain structure, it is tempting to suggest that error observation and error execution also rely on this simulation hypothesis. Namely, by simulating each other's behaviour we can recognize each other's errors and anticipate them. In this study we tested whether errors that cannot be simulated (machine errors) also evoke pMPFC activity. In other words, is pMPFC activation in error observation directly linked to simulation or not? Our data clearly show that both error types (human errors and machine errors) evoke pMPFC activity. In sum, pMPFC activation does not distinguish between the observation of human and machine errors. This highlights the general and non-social nature of the cognitive system that is responsible for the processing of errors.

Since both erroneous and non-erroneous unexpected events (i.e., machine errors and expectation condition) elicit pMPFC activation, our data suggest a more general role for the pMPFC. That is, pMPFC activation is related to a violation of expectancies of the observed events. The dominant views on pMPFC functioning posit that it signals response conflict (Botvinick, Braver, Barch, Carter, & Cohen, 2001), predicts error likelihood (Brown & Braver, 2005), or signals an outcome that is worse than expected (Holroyd & Coles, 2002). Recently however, a unitary account reconciling these views has been proposed (Alexander & Brown, 2010), relating the pMPFC to learning and to the prediction of outcomes of actions. In this view, both the non-occurrence of a predicted outcome and the occurrence of an unpredicted outcome (as is the case in the machine error condition and the expectancy condition) should evoke pMPFC activity (see also the orienting account, Notebaert, Houtman, Van Opstal, Gevers, Fias, & Verguts, 2009; Núñez Castellar, Kuhn, Fias, & Notebaert, 2010). Interestingly, our data pattern fits nicely with the predictions of this new account. The fact that the machine error condition and the expectation condition represent unexpected events is further supported by the anterior insular activity in these conditions (See Table 1). It has been argued that the insular activity can be seen as an orienting response (i.e., an arousal response to salient events) towards an error or unexpected event (Ullsperger, Harsay, Wessel, & Ridderinkhof, 2010).

Our data show that pMPFC activation is not uniquely related to the observation of errors that can be simulated. However, there might be other brain regions that distinguish between the observation of human errors and machine errors. To address this question, we directly compared brain activity related to human errors with brain activity related to machine errors. Note that the only difference between these conditions is the accuracy of the human action, (i.e., in the human error condition an incorrect action is performed whereas in the machine error condition the correct action is performed). First, subtracting human error activity from machine error activity did not reveal any significant brain activation. We can thus conclude that there are no specific brain regions involved in the processing of machine errors compared to human errors. However, when substracting machine errors from human errors, we found activation in the lateral occipitotemporal cortex (LOTC) including EBA and the human MT+ complex. These regions have been found to correlate with body-related visual perception (Downing et al., 2006; Weiner et al., 2011). In addition, the PMC and more specifically the frontal eye fields (FEF) were active. Also these areas are involved in visual processing or visual attention (Donner, Kettermann, Diesch, Ostendorf, Villringer, & Brandt, 2002; Muggleton, Kalla, Juan, & Walsh, 2011). Finally, besides these lower level areas of visual processing we also found two sites of activation in the parietal lobe (SPL and IPL). The SPL has been shown to be involved in body transformation processes and in action observation (Bonda, Petrides, Frey, & Evans, 1995; Calvo-Merino, Glaser, Grezes, Passingham, & Haggard, 2005; Urgesi, Calvo-Merino, Haggard, & Aglioti, 2007). Further, the IPL has been well documented in the area of action observation and has been linked to the mirror system (for a review see Cattaneo & Rizzolatti, 2009). In sum, the observation of an incorrect action seems to trigger regions related to the observations of human actions in a stronger way than the observation of correct actions.

Overall, it seems that pMPFC activity is not uniquely related to the observation of human errors but rather to the occurrence of unexpected events. Further, there are specific brain regions involved in the processing of human errors compared to machine errors. In general, we found areas related to visual processing (such as LOTC and FEF) and areas related to higher levels of visual processing (i.e., areas involved in action observation such as the IPL and SPL). These latter results suggest that the observation of an incorrect action stronger activate the brain mechanisms needed for understanding the action than the observation of correct actions.

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APPENDIX A

Situation	Correct	Human error	Machine error	Expectation	Question
Coffee machine	- cup is positioned in the machine - button 'one cup' is pressed - coffee is poured into the cup	- cup is positioned in the machine - button 'two cups' is pressed - coffee is spilled	- cup is positioned in the machine - button 'one cup' is pressed - coffee is spilled	- cup is positioned in the machine - button 'one cup' is pressed - coffee is poured into the cup and a picture of a ship is shown at the bottom left corner of the screen	What happened in the movie? - button 'one cup' was pushed, coffee was spilled - button 'one cup' was pushed, coffee was not spilled - button '2cups' was pushed, coffee was spilled - button '2 cups' was pushed, coffee was not spilled
Elevator	- person with suitcase enters elevator - person pushes button to close the door - elevator door closes	- person with suitcase enters elevator - person pushes button to close the door - suitcase prevents elevator door from closing	- person with suitcase enters elevator - person pushes button to close the doors - elevator door does not close entirely	- person with suitcase enters elevator - person pushes button to close the door - elevator door closes and a picture of a green bucket is presented at the right upper corner of the screen	What happened in the movie? - the suitcase was stuck between the door, but eventually the door closed - the suitcase was stuck between the door, and the door did not close - the suitcase was not stuck between the door and the door closed - the suitcase did not prevent the door from closing but the door did not close
Photocamera	- person switches on camera - button is pressed - flower is correctly photographed	- person switches on camera - button is pressed but finger is placed before the camera - flower is photographed but finger is also on the photograph	- person switches on camera - button is pressed - flower is photographed but there is a technical error in the picture	- person switches on camera - button is pressed - flower is correctly photographed and a picture of a blue car is shown at the upper right corner of the screen	What was displayed on the photograph? - an exact print of the flower - a technical incorrect print of the flower - a print of the flower with a finger superimposed on it - the windowsill

Electronic garage door	- person enters the correct code to open the garage door. (code is written on a piece of paper - 4455) - door opens	- person enters the wrong code - door does not open	- person enters the correct code - door does not open	- person enters the correct code - door opens and a picture of a black shoe is visible at the bottom right corner of the screen	What happened in the movie? - code 4455 was pushed, door opened - code 4455 was pushed, door did not open - code 5566 was pushed door opened - code 5566 was pushed, door did not open
Semi-automatic doors	- person holds the correct badge before the doors - doors open and person walks in	- person holds a bank card before the doors - doors do not open	- person holds the correct badge before the doors - doors do not open	- person holds the correct badge before the doors - doors open and person walks in at the same time a picture of a ninepin is shown at the upper right corner of the screen	What happened in the movie? - a bank card was scanned, the doors did not open - a bank card was scanned, the doors opened - the correct badge was scanned, the doors did not open - the correct badge was scanned, the doors opened
Vending machine	- person wants to have a cola (in her hand there is a note that specifies which drinks should be obtained) - the button for 'cola' is pushed and the cola is delivered	- person wants to have a cola - the button for 'fanta' is pushed and the fanta is delivered	- person wants to have a cola -the button for 'cola' is pushed but a fanta is delivered	- person wants to have a cola - the button for 'cola' is pushed and a cola is delivered, at the same time a picture of a house is presented at the upper left corner of the screen	What happened in the movie? - the button 'cola' was pushed, cola was delivered - the button 'cola' was pushed, fanta was delivered - the button 'fanta' was pushed, cola was delivered - the button 'fanta' was pushed, fanta was delivered
Photocopier	- person places image of a cat in the scanner part of the machine	- person places image of a cat in the scanner part of the machine, however only half of	- person places image of a cat in the scanner part of the machine	- person places image of a cat in the scanner part of the machine	What was displayed on the copy? - a dog

	- the copy button is pushed - a copy of the image is printed	the image is placed in the scanner part - the copy button is pushed - a copy of half of the image is printed	- the copy button is pushed - a copy is printed, however the colours of the image are inversed compared to the original image	- the copy button is pushed - a copy of the image is printed and a picture of a lamp is shown at the bottom right corner of the screen	- an exact copy of the image - half of the image - a copy of the image with inverted colours
Digital clock	- person verifies the hour on her watch (06:00) - the digital clock is set to 06.00 - digital clock shows 06.00	- person verifies the hour on her watch (06.00) - the digital clock is set to 03.00 - digital clock shows the wrong hour: 03.00	- person verifies the hour on her watch (06.00) - the digital clock is set to 06.00 - digital clock jumps to the wrong hour: 03.00	- person verifies the hour on her watch (06:00) - the digital clock is set to 06.00 - digital clock shows 06.00 and a picture of a chair is shown at the bottom left corner of the screen	What happened in the movie? - the clock was set at 03.00 but jumped to 06.01 - the clock was set at 03.00 and stayed at 03.00 - the clock was set at 06.00 and jumped to 03.01 - the clock was set at 06.00 and stayed at 06.00

CHAPTER 6

GENERAL DISCUSSION[1]

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[1] Parts of this chapter are published in Desmet, C., Fias, W., & Brass, M. (2011). Performance monitoring at the task and the response level. *Reviews in the Neurosciences, 22*(5), 575-581.

INTRODUCTION

In daily life we constantly adjust our behaviour according to the flexible demands of the environment. Situations of conflict and errors form key aspects for these behavioural adjustments. Moreover, a situation of conflict or an error signals that the current behaviour is no longer appropriate and that adjustments are needed. Over the past decades an innumerable amount of studies on error and conflict monitoring have emerged. However, this current research has approached errors and conflict from a narrow point of view. In my opinion, three different aspects of error and conflict processing should be addressed to broaden the perspective on this research. First of all, the classical literature has focused on errors and conflict at one specific level, namely the response level. Therefore, conclusions obtained via this research might not hold at different levels. We investigated this question in chapter two and three by extending research on errors and conflict to another level, namely the task level. Second, even when only considering research on the response level, the paradigms used in the field are very restricted. Moreover, in typical conflict tasks the fact that we can learn from our errors is neglected, typically, because there is not much to learn in these tasks. Since it is widely known that people learn from their errors, one can wonder if the results obtained in these simple tasks are indicative for our daily life behaviour. We answered this question in chapter four by studying behavioural correlates of error and conflict processing in a task where learning is possible, namely mental arithmetic. Third, over the last decade it has been found that the brain region involved in error execution is also active when observing errors. As a result, it has been suggested that we understand each other’s errors by means of internal simulation (e.g., Bates, Patel, & Liddle, 2005; Bekkering, de Bruijn, Cuijpers, Newman-Norlund, van Schie, & Meulenbroek, 2009; van Schie, Mars, Coles, & Bekkering, 2004). However until now, only the observation of human errors has been investigated. In chapter five we extended the research on error observation by investigating if other sorts of errors, namely errors caused by machines, also activate this particular brain region. In the current and last chapter of this thesis, I will provide an overview of the empirical results obtained in chapters 2, 3, 4 and 5 and will integrate these findings in light of the existing literature.

PREPARING OR EXECUTING THE WRONG TASK: THE INFLUENCE ON SWITCH EFFECTS

The goal of the second chapter was to establish a design in which we could disentangle task and response errors. Behavioural studies on task and response errors have been conducted before (Steinhauser & Hübner, 2006; Steinhauser & Hübner, 2008). However, in these paradigms, bivalent stimulus-response mappings were used. As a result, the different error types could not be disentangled univocally. For example, when performing a magnitude and a parity task and the responses ‘odd’ and ‘< 5’ are mapped onto one effector, task errors and correct responses cannot be distinguished for stimuli that are smaller than 5 and odd or for stimuli that are larger than 5 and even. Under the same condition, task errors cannot be distinguished from response errors for stimuli that are smaller than 5 and even or for stimuli that are larger than 5 and odd. To address this issue we used univalent stimulus-response mappings as in Meiran and Daichman (2005). In contrast to bivalent mappings, this allows one to infer from the subjects’ responses which error was made. In our design, the responses were divided over the index and the middle finger of the left and right hand. An error performed with the correct hand signified a response error, while an error performed with the wrong hand was classified as a task error or as a combination of a task and a response error (dependent on which finger was used). Further, we included two manipulations to increase the rate of response and task errors, respectively. To increase the response error rate, we presented flanker stimuli at both sides of the target. Response times were shorter on congruent flanker trials than on incongruent flanker trials. However, response errors were not affected by the congruency of the flankers. Despite the absence of a relation between response errors and flankers, overall we did obtain a sufficient response error rate (10%). Task error rate was effectively increased by the within switch manipulation. More precisely, if we inserted a switch cue after the occurrence of the stimulus more task errors were made than when participants did not had to switch tasks within the trial. Interestingly, we could replicate the behavioural findings obtained earlier for task and response errors. That is, Steinhauser and Hübner (2006) observed switch benefits instead of switch costs after task errors. They explained this effect by stating that response execution will strengthen the current task activations. In other words, when a task error is made the wrong task is strengthened, leading to a benefit on a subsequent task switch (since the previously strengthened task is presented again). Although we replicated this effect on the overall level, the effect disappeared after task errors made on within switch trials. At first this finding seems puzzling since one would expect to find the most robust effect in the condition where most task errors occurred (i.e., in the within switch condition). Since the within switch trials encompassed two task indications (one indicated by the first cue and one indicated by the secondary switch cue) we argued that both task indications might have influenced switch effects on the next trial, one leading to switch costs (indicated by the first cue) and one leading to switch benefits (indicated by the secondary cue). Hence, switch benefits after within switch trials might have been cancelled out. In a further experiment this prediction was confirmed. We showed reduced switch costs when on the previous trial two tasks were prepared. In sum, not only the executed task but also the task that was only prepared influences further switch effects. This is an important finding since most task switching studies have focused exclusively on the role of the executed task on subsequent switch costs (e.g., Philipp, Jolicoeur, Falkenstein, & Koch, 2007; Schuch & Koch, 2003; Verbruggen, Liefooghe, & Vandierendonck, 2006). We show here, that it is not necessary to execute a task to influence further behaviour.

ERRORS AND CONFLICT AT THE TASK LEVEL AND THE RESPONSE LEVEL

In chapter three we used the experimental design of chapter two to study neural correlates associated with task errors and task conflict in order to compare them with the neural correlates of response errors and response conflict. Since the flanker manipulation used in chapter two did not influence the response error rate, we decided to use another manipulation to increase response errors. In line with the within switch manipulation for task errors we inserted a response switch manipulation. Three trial types were thus implemented, no switches, a switch to the different task or a switch to the different response. The results indicated that task errors were effectively increased by the task switch cue and the response errors by the response switch cue.

AN ANATOMICAL SUBLOCALIZATION OF THE pMPFC

The neural results indicate that different subregions of the pMPFC are correlated with task errors, task conflict, response errors and response conflict. An overview of the different activations in relation to the pMPFC can be found in Figure 1.

As is apparent from the figure, the region activated by response conflict (in BA 8) was in line with regions earlier reported in the literature (for a review see Ridderinkhof, Ullsperger, Crone, & Niewenhuis, 2004). Response errors were associated with activation in BA 8 - BA 9. Although this activation is more dorsal and anterior than the activity usually reported, the distinction between response conflict and response errors resembles earlier findings. That is, response conflict activates more dorsal and posterior regions than response errors (Ridderinkhof et al., 2004; Ullsperger & von Cramon, 2004). Task conflict activated more posterior regions (preSMA) as already found in previous studies (Brass & von Cramon, 2002; Crone, Wendelken, Donohue, & Bunge, 2006; Rushworth, Hadland, Paus, & Sipila, 2002). Interestingly, we also obtained neural correlates for task errors, which have never been investigated before. As can be seen from Figure 1, task errors tend to activate a subregion of the pMPFC that is located anterior to the preSMA and more dorsal to the RCZ, which we labeled the dorsal frontomedian cortex (dFMC).

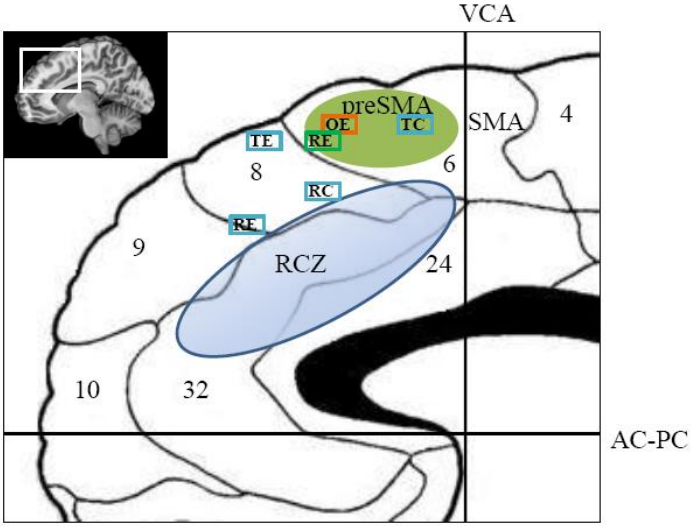

Figure 1. Midsaggital view of the pMPFC bordered by the VCA line and the AC-PC line. Two subregions of the pMPFC are indicated; preSMA is presented in green, RCZ is presented in blue. Brodmann areas are indicated with their corresponding number. Peak coordinates in the pMPFC related to task errors (TE), task conflict (TC), response errors (RE) and response conflict (RC) are indicated by blue squares. Further, activation related to response errors in the preSMA is indicated by a green square. Finally, observation of errors and unexpected events is indicated by an orange square.

Although the pattern of results seems to indicate dorsal-ventral and anterior-posterior distinctions in the pMPFC, there is one activation that does not fit our interpretation. Moreover, we also obtained a dorsal component, in the preSMA, related to response errors (indicated by a green square in Figure 1). This might be related to the fact that response errors were elicited by a switch manipulation. Activation related to response errors might thus reflect a switch process (reflected by the preSMA activity) and an error related process (reflected by the ventral activity in the pMPFC).

There are some studies that already addressed different sublocalizations in the pMPFC. However these studies are primarily restricted to conflict research. For example, some studies have shown distinctions between forms of pre-response conflict and response conflict. It seems that pre-response conflict is associated with more dorsal and posterior parts of the pMPFC than response conflict (Kim, Kroger, & Kim, 2011). Others have shown an anterior to posterior typology ranging from strategy control over decision control towards response control (Venkatraman, Rosati, Taren, & Huettel, 2009). Also, decision conflict without response conflict seems to activate regions in the pMPFC more dorsal than those usually found for response conflict (Pochon, Riis, Sanfey, Nystrom, & Cohen, 2008). More related to our distinction of task and response conflict, Orr and Weissman (2009) presented a cue and a target in two modalities at the same time (visual and auditory modality). At cue level, the visual modality informed participants to which feature of the target (look or hear) they should react. The target comprised a spoken and a visually presented ‘x’ or ‘o’. The authors found that conflict between the visual and the auditory information at a cue level (which represents a conflict between tasks) activated dorsal parts of the pMPFC while conflict at a target level (which represents conflict at the response level) activated ventral parts of the pMPFC. While different levels of conflict (see also Egner, 2008) and their corresponding brain areas have been discussed in the literature, different levels of error processing have been widely neglected. Previously, Krigolson and Holroyd (2007) reported a dissociation between high and low level errors. They manipulated these two levels of error processing in a movement tracking task. Participants were required to move a cursor from a start point to a target point by manipulating a joystick. However, the target point sometimes changed to a different location, resulting in low level errors. In some cases, participants could not move the cursor making it impossible to achieve the movement goal. These cases were labeled as high-level errors. The authors showed by means of ERP measurements that the frontal brain system is related to high-level errors while the posterior system is correlated with low level errors. Another interesting study, more related to our distinction of task and response errors, is the study of Nee, Kastner and Brown (2011). These authors contrasted effects of response conflict, response errors and task switching to investigate sublocalizations in the pMPFC. Interestingly their manipulation of task switches can be seen as a task error manipulation. More precisely, on each trial a face and a body part was presented. Body and face parts could be human or monkey. During the face task the species of the face should be classified and likewise for the body task. Response conflict was thus induced by the species congruence of the irrelevant feature. The task that had to be executed was only indirectly indicated by feedback. More precisely, the authors presented runs of the same task of 5-15 trials. When a task switch had to be made, participants received negative feedback. In other words, task switch trials were characterized by a wrong task performance or a task error. Although activity for response errors, response conflict and task switches (or task errors) overlapped largely, the cluster found for task switches extended more dorsally and posterior in the pMPFC than for response conflict. Further replicating our results, activity for response errors extended more ventral and anterior in the pMPFC than activity for task switches. In contrast to what we found, task switches (or task errors), did not show differential activation compared to response errors. However, one should bear in mind that task errors in the study of Nee et al. (2011) might primarily reflect an orienting response, since the error could only be deduced from negative feedback. Apart from these studies and our own experiment in chapter 3, there seems to be no research concerning the sublocalization of errors in the brain. However, the task error region that we described in the pMPFC, namely the dFMC, has been described before in higher level decision processes (Elliott & Dolan, 1998; Goel & Dolan, 2000; Rushworth et al., 2002; Volz, Schubotz, & von Cramon, 2003; Volz, Schubotz, & von Cramon, 2004). Based on these findings, and keeping in mind the different connections of the pMPFC to motor output, we argue that more abstract errors are processed in more dorsal regions of the pMPFC.

ERROR ADAPTATION IN MENTAL ARITHMETIC

POST-ERROR SLOWING AND POST-ERROR ACCURACY INCREASE

In chapter four we tested whether the same behavioural effects observed in typical laboratory or simple mapping tasks would also be observed in a more daily used task such as mental arithmetic. As we already stated in the introducing chapter, classical accounts of error monitoring posit that people will shift their point on the speed-accuracy trade off after encountered with an error. That is, they will become slower but more accurate. Although post-error slowing is a very robust effect, it does not always coincide with accuracy increases. This forms a problem for classical theories of error monitoring and questions the adaptive nature of post-error slowing. Recent studies have showed that post-error slowing is not restricted to the occurrence of an error but rather to the occurrence of an unexpected event. Indeed, post-correct slowing is observed when errors are more frequent than correct responses. Likewise, slowing is observed after oddball events (Notebaert, Houtman, Van Opstal, Gevers, Fias, & Verguts, 2009). These findings indicate that the occurrence of an error or an unexpected event captures attention and slows down subsequent task processing. This explanation of post-error slowing fits nicely with the behavioural results of the study by Jentzsch and Dudschig (2009). These authors showed that after an error central resources are occupied for a certain period of time. Moreover, the authors observed an underadditive effect of perceptual difficulty and post-error slowing. That is, while perceptual difficulty led to worse performance after correct trials, this performance difference was absent after error trials. This underadditivity was explained by the fact that the perceptual discrimination process could be carried out in parallel to the error monitoring process. Hence, after errors the difference between easy and difficult perceptual discriminations was absorbed into this waiting period (under the assumption that perceptual processes can be carried out in parallel to central processes). Although the authors refer to this time period as an error monitoring process during which accuracy of the response is monitored, their data could also be explained by an orienting account. Moreover, after an error there is a certain time period not available for further task processing due to an orientation process. Interestingly, this hypothesis could be tested by investigating the underadditive effect found by Jentzsch and Dudschig (2009), after other infrequent events such as oddballs, or infrequent correct responses. If the monitoring process is specific to the monitoring of the error, one should only find the underadditivity effect after errors. If, on the other hand, the monitoring process is a more general orientation process one should observe the effect after all sorts of infrequent events.

There is thus converging evidence that post-error slowing might not be related to adaptive processes but might rather reflect an attentional process. This would explain why post-error slowing is not always accompanied by performance improvements. More specifically, post-error slowing is an attentional effect and post-error accuracy increase is an adaptive effect. However, this does not answer the question why performance improvements are not always observed after errors. One would think that people tend to learn from earlier mistakes and thus improve their performance. In chapter four we showed that one of the reasons for the absence of post-error accuracy increases might be that most error monitoring tasks are very restricted in the behavioural adaptations they allow. Consequently, post-error adaptations might not be revealed in these tasks. When we used a task that allowed a more rich set of behavioural adaptations we succeeded to find post-error accuracy increases. This finding shows that it is important to use a wide range of experimental paradigms when studying post-error effects. Of course, the question remains why previous studies, using the same restricted set of experimental paradigms, sometimes observed post-error accuracy increases while other’s did not. An important factor that has been largely neglected in this research and that can account for the differences between studies are individual differences. In a very recent study, Moser and colleagues (2011) showed that beliefs about learning or intelligence have an impact on the way we monitor our errors. More specifically, they showed that while these beliefs did not interact with post-error slowing, this was the case for post-error accuracy increases. Moreover, post-error accuracy increases were positively correlated with how strong people believed intelligence is malleable and can be developed through learning (Moser, Schroder, Heeter, Moran, & Lee, 2011). In sum, testing behavioural correlates of post-error behaviour with a wider range of paradigms and taking into account individual differences can shed more light on the adaptive nature of these correlates.

CONFLICT ADAPTATION

Further, we found no evidence for conflict adaptation in mental arithmetic. This is in line with what we predicted and can be explained by a general ‘adaptation by binding’ account (Verguts & Notebaert, 2009). According to this account, situations of conflict lead to arousal which will strengthen the active task representations. This account combines earlier discrepant theories concerning the conflict adaptation effect described in chapter one. Moreover, it has been questioned if the conflict adaptation effect was a cognitive control effect or merely the result of feature binding processes. The ‘adaptation by binding’ account reconciles these views by postulating cognitive control as a combination of arousal and binding processes. As regards our data, the account predicts that strengthening a certain multiplication due to conflict (e.g., 4 x 6 = 30) will not lead to improved performance on a different multiplication trial (e.g., 7 x 8 = 49), explaining the absence of conflict adaptation.

THE ROLE OF THE MEDIAL PREFRONTAL CORTEX IN ERROR OBSERVATION

SALIENCY OF EVENTS

Finally in chapter five we studied neural correlates associated with error observation. We found that the pMPFC did not distinguish between errors induced by humans or errors induced by machines. We even found the most extensive area of activation in the pMPFC when observing an unexpected event. From the error execution domain there is now converging evidence that the role of the pMPFC is not solely dedicated to error processing but might rather comprise a more general role. For example in the study of Braver and colleagues (2001) pMPFC activation was found under different situations of low frequency behaviour. More precisely, pMPFC activation was found during low frequency events across three different tasks, namely response inhibition, target detection and response selection (Braver, Barch, Gray, Molfese, & Snyder, 2001). Likewise Jessup, Busemeyer and Brown (2010) showed in a gambling task that the pMPFC only responded to losses when these were infrequent. When losses were more likely than wins, the pMPFC effect reversed. That is, pMPFC responded to wins instead of losses. Oliveira, McDonald and Goodman (2007), showed that the FRN (feedback related negativity), an ERP correlate associated with pMPFC activation, was not related to the valence of the feedback but rather to the violation of expectancy. Moreover, the FRN could be induced by positive feedback when this was unexpected. Analogue, when negative feedback was expected no FRN was observed. In line with these results, in chapter five we observed pMPFC activity related to deviations of expectancy. That is when observing an unexpected behaviour such as an error the pMPFC was activated. However, when observing a non-erroneous unexpected event (i.e., an unrelated stimulus appearing on the screen), the most extensive pMPFC activity was revealed. Although one should bear in mind that our study comprises an error observation study and not an error execution study, our data underline the role of pMPFC in detecting salient events rather than errors per se.

The attribution of this broader role to the pMPFC does not fit with the computational models described in the introduction. First, the role of the pMPFC is not restricted to a detector of conflict, arguing against the conflict monitoring account (Botvinick, Braver, Barch, Carter, & Cohen, 2001). Second, although the outcomes are not expected they are not necessarily worse than expected. Indeed, as described above also positive expectations lead to pMPFC activation (Jessup et al., 2010). Hence, the learning reinforcement theory (Holroyd & Coles, 2002) does not capture this more general role of the pMPFC. In the same line, the error prediction model (Brown & Braver, 2005) does not explain why pMPFC is activated by positive outcomes. Recently, a new computational model was suggested that can account for the data obtained in this thesis and from the studies described above. According to this account the pMPFC learns to predict possible outcomes of an action and signals discrepancies between actual and expected outcomes (Alexander & Brown, 2010). The pMPFC thus responds to negative but also to positive unexpected events.

AN ANATOMICAL SUBLOCALIZATION OF THE PMPFC

The region in the pMPFC that we found to correlate with error observation is more dorsally located than the region normally described in error execution studies. Indeed, when comparing the coordinates obtained in chapter five with the meta-analysis of Ridderinkhof and colleagues (2004), our peak coordinates are more dorsally located than those obtained for error execution studies, more precisely in the preSMA, see Figure 1. Since the observation of errors will not automatically activate the correct response, this fits well with what we postulated in the discussion of chapter three. Moreover, errors that are directly related to a motor response will activate more ventrally located subparts of the pMPFC, while more abstract errors such as task errors or observed errors will activated more dorsal parts of the pMPFC. In light of this latter argument it would be very interesting to investigate brain activity related to observed errors that evoke a response from the observer. In daily life one can think of numerous examples where we directly act upon the errors of others. For example when someone stumbles while holding an expensive vase, we will probably try to catch the vase.

SPECIFIC BRAIN REGIONS ASSOCIATED WITH OBSERVING HUMAN ERRORS

Outside the pMPFC, the observation of human errors activated a unique activation pattern compared to machine errors. More precisely, areas involved in visual processing and action understanding such as the inferior parietal lobe (IPL) and the lateral occipitotemporal cortex (LOTC) were only activated when observing human errors. When contrasting machine errors with human errors no unique activation was revealed. This reflects that the observation of human errors causes strengthened activation in regions related to the visual processing of body related characteristics.

A BROADER PERSPECTIVE

To study our complex cognitive abilities, experimental psychologists try to reconstruct daily life situations in the laboratory by means of simple computer tasks. When results are replicated over these laboratory tasks, it is considered legitimate to extrapolate laboratory findings to our daily life cognitive abilities. The standard procedure to study error and conflict processing in the laboratory comprises simple computer tasks where conflict at a response level is induced. At a neural level, the pMPFC, and in particular the RCZ, is considered the core region of error and conflict processing (Ridderinkhof et al., 2004; Ullsperger & von Cramon, 2004). In addition, the pMPFC is activated when we observe other humans making errors. At a behavioural level, post-error slowing and conflict adaptation are considered robust effects, revealing adaptation after conflict or errors (e.g., Botvinick et al., 2001; but see also Notebaert et al., 2009). However, in this thesis I demonstrate that always using the same restricted set of paradigms might have biased these conclusions and thus might have biased our knowledge about human error and conflict processing.

First of all, when studying neural correlates of error processing at a different level than the commonly studied response level, different neuro-anatomical regions are revealed. More precisely, we demonstrated that more abstract events are related to more dorsal parts of the pMPFC, while events that are more related to a motor response will activate more ventral parts of the pMPFC. Recent work confirms that the pMPFC is indeed related to subsequent adjustments in behaviour. Moreover, it was shown that pMPFC activity predicted signal increases in perceptual areas encoding task relevant features and signal decreases in perceptual areas encoding task irrelevant features (Danielmeier, Eichele, Forstmann, Tittgemeyer, & Ullsperger, 2011). One interesting topic for future research is to see if dissociable adaptation processes are triggered by different subparts of the pMPFC. More specifically, in accordance with what we hypothesized the subregion in the pMPFC related to task errors might trigger brain areas related to general task processing as found in task switching literature (e.g., Brass & von Cramon, 2002; Crone et al., 2006; Dove, Pollmann, Schubert, Wiggins, & von Cramon, 2000; Hyafil, Summerfield, & Koechlin, 2009; Ruge, Brass, Koch, Rubin, Meiran, & von Cramon, 2005; Rushworth et al., 2002) while the subregion in the pMPFC related to response errors might trigger perceptual brain areas as shown before (Danielmeier et al.,2011; King, Korb, von Cramon, & Ullsperger, 2010).

Second, due to the over-simplification of tasks on error processing, one of the key features of error processing (i.e., learning from errors) might not be revealed. In other words, if there is nothing to learn, one cannot measure correlates of learning. Indeed, when using a task where learning is possible, namely mental arithmetic, different behavioural effects were found than in the typically used paradigms.

Third, we showed that the region previously believed to be dedicated to the processing of human errors is also active when observing machine errors. In addition, we demonstrated that the pMPFC is active when observing salient events, erroneous or not. This latter finding contradicts the simulation account and illustrates again that it is important to approach errors from a broader perspective.

CONCLUSION

In this thesis I aimed to widen the current perspective on error and conflict processing. The conclusions of this thesis are threefold. First of all, we demonstrated that pMPFC does not entail a unitary function. Moreover, we showed that errors and conflict at response and task levels can be dissociated in the pMPFC. Further, we demonstrated that behavioural effects that have been extensively described and have served as evidence for human adaptive control, might be restricted to a specific class of experimental paradigms. Finally, we showed that pMPFC is not solely related to the observation of errors, but also to the observation of unexpected events. In sum, we show that adaptive control should be investigated at different levels in a wider range of experimental tasks and that error observation research should not exclusively focus on human errors.

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CHAPTER 7
NEDERLANDSTALIGE SAMENVATTING

INLEIDING

Eén van de meest kenmerkende menselijke eigenschappen is onze imperfectie, of het feit dat we af en toe fouten maken. Meestal hebben deze fouten geen verdragende consequenties en halen we er zelfs informatie uit om ons gedrag te verbeteren. Met andere woorden, foutgerelateerde gedragingen vormen een belangrijk onderdeel van menselijk adaptief gedrag. Het is dan ook niet verwonderlijk dat foutverwerking een uitvoerig bestudeerd domein in de cognitieve psychologie omvat (voor een overzicht zie Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004; Ullsperger & von Cramon, 2004). In het laboratorium gebruikt men simpele conflict taken om fouten uit te lokken. Typisch in deze taken is dat participanten een respons uitvoeren terwijl irrelevante informatie met deze respons interfereert. In de flanker taak (Eriksen & Eriksen, 1974) bijvoorbeeld moet de richting van een centrale pijl aangegeven worden, terwijl deze pijl geflankeerd wordt door twee andere pijlen. In een conflict situatie zullen deze flankerende pijlen in een andere richting wijzen dan de centrale pijl en dus de verkeerde respons activeren. Door deze situatie van conflict zullen meer respons fouten gegenereerd worden dan in een niet-conflicterende situatie. Respons fouten en respons conflict komen dus heel vaak samen voor.

Hoewel de literatuur naar fouten en conflict heel uitgebreid is, zijn fouten en conflict vanuit een enkelvoudig standpunt bekeken. Ten eerste heeft fout onderzoek tot hier toe voornamelijk gefocust op één niveau, namelijk fouten op een respons niveau. Verder heeft huidig onderzoek voornamelijk gebruik gemaakt van eenvoudige taken die niet altijd weergeven wat er in de werkelijkheid gebeurt. Ten slotte, zijn de neurale correlaten van foutobservatie enkel onderzocht tijdens het observeren van menselijke fouten. In deze doctoraatsthesis zal ik fouten en conflict uit een bredere invalshoek benaderen. Daartoe zal ik achtereenvolgens de drie voorvermelde punten behandelen. Ten eerste zullen we onderzoeken of fouten en conflict op het taak niveau dezelfde hersen gebieden activeren als fouten en conflict op een respons niveau. Ten tweede zullen we kijken of dezelfde gedragseffecten die gevonden worden in experimentele taken ook teruggevonden worden in taken die complexer zijn en aldus meer overeenkomen met de werkelijkheid. Ten slotte zullen we onderzoeken of het neuraal systeem dat verantwoordelijk is voor het observeren van fouten, enkel actief is bij de observatie van een menselijke fout of ook reageert op fouten gemaakt door machines.

EERDERE BEVINDINGEN

GEDRAGSEFFECTEN

Op gedragsniveau zijn een aantal robuuste effecten gevonden na het maken van een fout of na het optreden van conflict. Ten eerste is er geobserveerd dat participanten trager zijn na een fout dan na een correct antwoord (e.g., Laming, 1968; Rabbitt & Rodgers, 1977). Deze vertraging werd aanzien als evidentie voor een aanpassing in controle na een fout, of anders gezegd als een adaptief effect. Na een fout zullen proefpersonen namelijk vertragen om zo minder fouten te maken op volgende proefbeurten. Hoewel proefpersonen vertragen na een fout, is een verbetering in performantie na een fout niet altijd terug gevonden (e.g., Hajcak, McDonald, & Simons, 2003; Hajcak & Simons, 2008; King, Korb, von Cramon, & Ullsperger, 2010). Dit stelt het feit dat de vertraging na een fout een adaptief effect is in vraag. Recent is er dan ook gesuggereerd dat de vertraging na een fout een aandachtseffect in plaats van een adaptief effect is (Notebaert, Houtman, Van Opstal, Gevers, Fias, & Verguts, 2009; Núñez Castellar, Kuhn, Fias, & Notebaert, 2010). Volgens deze visie is de vertraging na een fout niet gerelateerd aan de fout op zich, maar eerder aan het feit dat een fout een onverwachte gebeurtenis is. Deze onverwachte gebeurtenis trekt de aandacht weg van de taak die moet uitgevoerd worden en zorgt op die manier voor een vertraging (Notebaert et al., 2009).

Op het vlak van conflict verwerking is er een vermindering in interferentie gevonden na een conflict trial dan na een niet-conflict trial. Dit effect werd voor het eerst beschreven door Gratton en collega's in de flanker taak en wordt geïnterpreteerd als een cognitief controle effect (Gratton, Coles, & Donchin, 1992). Een conflict trial zal namelijk meer controle vragen en daardoor zullen op volgende trials de interferentie effecten verkleinen. Of dit effect nu werkelijk een marker is van cognitieve controle of eerder een bij-effect van stimulus-respons repetities is fel gedebatteerd (Hommel, Proctor, & Vu, 2004; Mayr, Awh, & Laurey, 2003; Nieuwenhuis, Stins, Posthuma, Polderman, Boomsma, & de Geus, 2006). Recent zijn deze twee visies bijeengebracht in de 'adaptatie door binding' theorie (Verguts & Notebaert, 2009). Volgens deze theorie is cognitieve controle een combinatie van arousal en binding processen. Een situatie van conflict zal resulteren in een toestand van verhoogde arousal en veroorzaakt op die manier een versterking van de geactiveerde taak representaties.

FUNCTIONELE NEURO-ANATOMIE VAN FOUTEN EN CONFLICT

Het meest beschreven hersen gebied in fout en conflict literatuur is gelokaliseerd in het posterieure en mediale gedeelte van de prefrontale cortex, verder de posterieure mediale prefrontale cortex genoemd (pMPFC). Dit gebied breidt zich dorsaal uit vanaf de AC-PC lijn, een lijn die de anterieure met de posterieure commissuur verbindt. De posterieure grens wordt bepaald door de VCA lijn, een verticale lijn die door de anterieure commissuur gaat en loodrecht staat op de AC-PC lijn. De Brodmann arealen (BA) die geassocieerd worden met de pMPFC zijn BA 6, BA 8, BA 9, BA 32 en BA 24, zie Figuur 1. De posterieure grens van de pMPFC kan eveneens aangeduid worden door een subregio van de pMPFC, namelijk de presupplementarische motor area (preSMA). Hoewel hersen activatie geassocieerd met respons fouten en respons conflict wijd verspreid is over de pMPFC, is de kern van activatie te vinden in de rostrale cingulate zone (RCZ) (voor een overzicht zie Ridderinkhof et al., 2004; Ullsperger & von Cramon, 2004). Volgens Picard en Strick (1996) strekt de RCZ zich anterieur uit vanaf de VCA lijn en beslaat het gebied voornamelijk BA 32. Hoewel het gebied ventraal tot in BA 24 en dorsaal tot in BA 8 en BA 6 reikt. Voor een overzicht van de anatomische labels zie Figuur1.

Of er een anatomische dissociatie bestaat in de pMPFC tussen fouten en conflict is nog steeds een open vraag. Sommige studies hebben aangetoond dat de RCZ geactiveerd wordt door zowel fouten als conflict (Carter, Braver, Barch, Botvinick, Noll, & Cohen, 1998; Kerns, Cohen, MacDonald, Cho, Stenger, & Carter, 2004). Andere hebben een distinctie in de pMPFC gevonden tussen fouten en conflict. Deze laatste studies vonden dat meer ventrale gebieden gerelateerd zijn aan respons fouten en meer dorsale gebieden gerelateerd zijn aan respons conflict (Braver, Barch, Gray, Molfese, & Snyder, 2001; Kiehl, Liddle, & Hopfinger, 2000; Ullsperger & von Cramon, 2001; Wittfoth, Kustermann, Fahle, & Herrmann, 2008). Deze relatie is in overeenstemming met de connecties van de pMPFC naar motor output. Ventrale delen van de pMPFC zijn immers meer gerelateerd aan de primaire motor cortex en het ruggenmerg, terwijl dorsale gedeelten meer gerelateerd zijn aan hersen gebieden die betrokken zijn in hogere orde cognitie (Ullsperger & von Cramon, 2001; Ullsperger & von Cramon, 2004). Aangezien fouten de correcte respons zullen uitlokken, is het plausibel dat ze meer gerelateerd zijn aan gebieden die gecorreleerd zijn met motor output dan respons conflict.

OVER HET RESPONS NIVEAU HEEN: TAAK CONFLICT EN TAAK FOUTEN

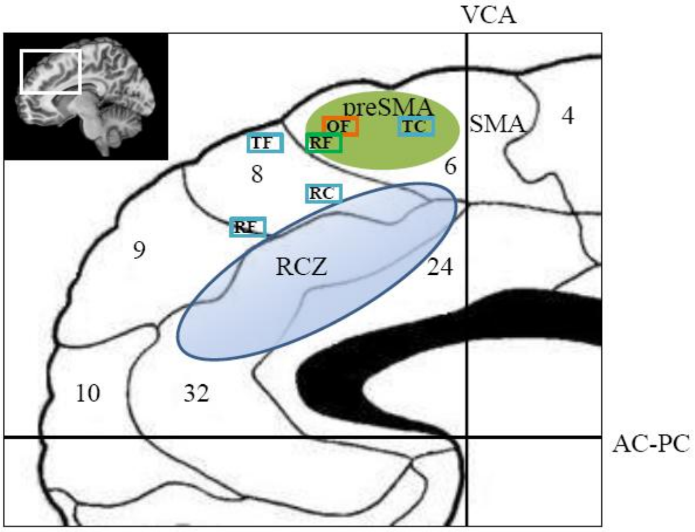
Tot hier toe hebben we literatuur beschreven omtrent fouten en conflict op een respons niveau. Conflict komt echter niet alleen voor op een respons niveau maar ook op een taak niveau. Verrassend genoeg is de literatuur rond taak conflict volledig geïsoleerd van literatuur rond respons conflict. Taak conflict is namelijk uitvoerig bestudeerd geweest met een andere klasse van paradigma’s, namelijk taak afwisselingsparadigma’s (Monsell, 2003). In deze paradigma’s voeren proefpersonen twee taken uit in een random of voorgeprogrammeerde volgorde. Een typische bevinding in dit onderzoek is een vertraging en slechtere prestatie op een taak wissel in vergelijking met een taak herhaling, de zogenaamde wisselkost (e.g., Monsell, 2003). Op neuraal vlak zijn verschillende hersen gebieden in een fronto-parietaal netwerk geassocieerd met taak afwisseling (Brass & von Cramon, 2002; Crone, Wendelken, Donohue, & Bunge, 2006; Dove, Pollmann, Schubert, Wiggins, & von Cramon, 2000; Hyafil, Summerfield, & Koechlin, 2009; Ruge, Brass, Koch, Rubin, Meiran, & von Cramon, 2005; Rushworth, Hadland, Paus, & Sipila, 2002).

DE VERKEERDE TAAK VOORBEREIDEN OF UITVOEREN: DE INVLOED OP SWITCH EFFECTEN

Hoewel er dus onderzoek bestaat naar respons fouten, respons conflict en taak conflict heeft tot onze verbazing geen enkele studie de neurale correlaten van taak fouten bestudeerd. In deze doctoraatsthesis vullen we deze lacune op. In **hoofdstuk twee** ontwikkelden we een design waarin taak fouten, taak conflict, respons fouten en respons conflict konden onderzocht worden. We voerden twee manipulaties in om het aantal respons en taak fouten te verhogen. Om respons fouten te verhogen presenteerden we flanker stimuli aan beide zijden van de target stimulus. Respons tijden waren korter op congruente dan op incongruente flanker trials. Echter, het aantal respons fouten werd niet beïnvloed door de flanker manipulatie. Ondanks dit laatste, vonden we over het experiment heen een voldoende aantal respons fouten (10%). Taak fouten werden effectief verhoogd door een taak wissel aan te bieden tijdens de trial. Meer specifiek, wanneer we een wissel cue na de verschijning van de stimulus presenteerden, werden meer taak fouten gemaakt dan wanneer proefpersonen niet moesten wisselen van taak tijdens de trial. Met dit paradigma repliceerden we de gedragseffecten die eerder gevonden werden voor taak en respons fouten. Net zoals Steinhauser en Hübner (2006), observeerden we wissel voordelen in plaats van wissel kosten na een taak fout. Deze bevinding werd verklaard door voornoemde auteurs door te stellen dat respons uitvoering de huidige taak activaties versterkt. Met andere woorden, wanneer een taak fout gemaakt wordt, wordt de verkeerde taak versterkt. Dit zal leiden tot een voordeel op de volgende trial (aangezien de vorige versterkte taak opnieuw wordt aangeboden). In additie toonden we aan dat niet enkel de uitgevoerde taak maar ook een taak die enkel voorbereid is, leidt tot wissel effecten op een volgende trial. Dit is een belangrijke bevinding aangezien de meeste taak afwisselingsstudies exclusief focussen op de rol van de uitgevoerde taak op volgende wissel kosten (e.g., Philipp, Jolicoeur, Falkenstein, & Koch, 2007; Schuch & Koch, 2003; Verbruggen, Liefooghe, & Vandierendonck, 2006).

NEUROLOGISCHE CORRELATEN VAN FOUTEN EN CONFLICT OP HET TAAK EN HET RESPONS NIVEAU

In **hoofdstuk drie** gebruikten we het paradigma ontwikkeld in **hoofdstuk twee** om de neurale correlaten geassocieerd met taak fouten en taak conflict te vergelijken met die van respons conflict en respons fouten. We vonden dat verschillende subregio’s van de pMPFC gecorreleerd waren met taak fouten, taak conflict, respons fouten en respons conflict. Een overzicht van de verschillende activaties in de pMPFC kan teruggevonden worden in Figuur 1. Het gebied geactiveerd door respons conflict (in BA 8) is in lijn met de gebieden gerapporteerd in de literatuur (voor een overzicht zie Ridderinkhof et al., 2004). Respons fouten waren geassocieerd met activatie in BA 8 - BA 9. Hoewel deze activatie dorsaler en meer anterieur is dan de activatie die normaal gerapporteerd wordt, repliceert het onderscheid tussen respons conflict en respons fouten eerdere bevindingen. Respons conflict activeerde namelijk meer dorsale en posterieur delen dan respons fouten (Ridderinkhof et al., 2004; Ullsperger & von Cramon, 2004). Taak conflict activeerde meer posterieure gebieden (preSMA) van de pMPFC zoals reeds werd gevonden in eerdere studies (Brass & von Cramon, 2002; Crone et al., 2006; Rushworth et al., 2002). Voor het eerst werden ook neurale correlaten voor taak fouten gerapporteerd. Taak fouten activeerden een subregio van de pMPFC die anterieur ligt ten opzichte van de preSMA en dorsaal ten opzichte van de RCZ.



Figuur 1. Midden sagittaal zicht van de pMPFC. Dit gebied wordt begrensd door de VCA lijn en de AC-PC lijn. Twee subregio's van de pMPFC zijn aangeduid; preSMA in het groen en RCZ in het blauw. Brodmann arealen zijn aangeduid met hun overeenkomstige nummers. Piek coördinaten in de pMPFC gerelateerd aan taak fouten (TF), taak conflict (TC), respons fouten (RF) en respons conflict (RC) zijn aangeduid met blauwe vierkanten. Verder is de activatie gerelateerd aan respons fouten in de preSMA aangeduid door middel van een groen vierkant. Activatie gerelateerd aan de observatie van fouten en onverwachte gebeurtenissen is aangeduid met een oranje vierkant (OF).

We noemden dit gebied de dorsale frontomediane cortex (dFMC). Eén activatie is niet in overeenstemming met het dorsaal-ventraal en anterieur-posterieur onderscheid in de pMPFC. We vonden namelijk ook een dorsale activatie (in de preSMA) voor respons fouten (aangeduid door een groen vierkant in Figuur 1). Dit kan te maken hebben met het feit dat respons fouten uitgelokt zijn door een wissel manipulatie. Activatie gerelateerd aan respons fouten kan dus enerzijds een wissel proces (gereflecteerd door de preSMA activiteit) en anderzijds een foutgerelateerd proces weergeven (gereflecteerd door de ventrale activatie in de pMPFC).

Het gebied dat we vonden voor taak fouten, namelijk de dFMC, werd eerder reeds beschreven in hogere orde beslissingsprocessen (Elliott & Dolan, 1998; Goel & Dolan, 2000; Rushworth et al., 2002; Volz, Schubotz, & von Cramon, 2003; Volz, Schubotz, & von Cramon, 2004). Hierop verder bouwend en de verschillende connecties van de pMPFC naar motor output in het achterhoofd houdend, kunnen we concluderen dat abstractere fouten in meer dorsale regio's van de pMPFC verwerkt worden.

FOUT EN CONFLICT VERWERKING IN HET LABORATORIUM

Tot nu toe heb ik een overzicht gegeven van de studies over conflict en foutverwerking op het respons niveau en op het taak niveau. Bijna al deze studies gebruikten heel simpele taken met een gelimiteerde ecologische validiteit. Zoals hierboven beschreven zijn conflict en fouten doorgaans bestudeerd in verschillende spatiale en non-spatiale compatibiliteitstaken, zoals de flanker taak (Eriksen & Eriksen, 1974), de Stroop taak (Macleod, 1991; Stroop, 1935) en de Simon taak (Simon, 1969). Zelfs al is een brede waaier aan paradigma's gebruikt, adaptief gedrag in deze taken is gelimiteerd tot een heel specifieke strategie. Na een fout in de flanker taak bijvoorbeeld, is de enige mogelijke strategie om de fout in de toekomst te vermijden, meer aandacht te besteden aan de centrale pijl. Echter, in vele situaties in het dagelijkse leven, zal een fout niet alleen een verhoging in aandacht veroorzaken maar ook een informatieve rol spelen. Wanneer we bijvoorbeeld een nieuwe vaardigheid aanleren zoals dansen of het bespelen van een muziekinstrument is het heel cruciaal om onze fouten te analyseren. Meer bepaald moeten we uitzoeken wat fout is gegaan om deze fout in de toekomst te kunnen vermijden. Dit leeraspect gaat verloren in typische laboratorium taken aangezien daar niet veel te leren valt. Als gevolg, kunnen huidige theorieën rond fout en conflict verwerking, de cognitieve operaties die gerelateerd zijn aan foutverwerking onderschatten.

In **hoofdstuk vier** hebben we dit probleem aangepakt door na-effecten van fouten en conflict te bestuderen in een cognitief uitdagendere taak, namelijk hoofdrekenen. Naast de typisch geobserveerde vertraging na een fout, vonden we ook evidentie voor een verbetering in performantie na een fout. Hier tonen we dus aan dat één van de redenen waarom verbetering na een fout niet altijd teruggevonden wordt, ligt aan de te restrictieve set van gedragsaanpassingen in laboratorium taken.

Verder vonden we geen evidentie voor conflictadaptatie in hoofdrekenen. Dit is in lijn met onze voorspellingen en komt overeen met de ‘adaptatie door binding’ account (Verguts & Notebaert, 2009). Volgens deze account leiden situaties van conflict tot arousal. Deze toestand van arousal zorgt dan voor een versterking van de actieve taak representaties. Voor onze data betekent dit dat de versterking van een bepaalde multiplicatie (e.g., 4 x 6 = 30) niet zal leiden tot een verbeterde performantie op een andere multiplicatie (e.g., 7 x 8 = 49).

HET OBSERVEREN VAN FOUTEN

Het laatste hoofdstuk van deze dissertatie focust op fout observatie. Recent neuro-wetenschappelijk onderzoek heeft aangetoond dat hetzelfde gebied dat betrokken is in foutverwerking, namelijk de pMPFC (Ridderinkhof et al., 2004; Ullsperger & von Cramon, 2004), ook actief is wanneer we fouten van anderen observeren. (de Bruijn, de Lange, von Cramon, & Ullsperger, 2009; Manthey, Schubotz, & von Cramon, 2004; Newman-Norlund, Ganesh, van Schie, de Bruijn, & Bekkering, 2009; Shane, Stevens, Harenski, & Kiehl, 2008). Het uitvoeren en het observeren van fouten steunen dus op dezelfde neurale mechanismen. Tot nu toe blijft het echter onduidelijk wat de reden voor dit gedeeld mechanisme is. Gedeelde activatie voor observatie en executie werd eerder gerapporteerd voor acties in het algemeen (voor een overzicht zie Rizzolatti & Craighero, 2004; Van Overwalle & Baetens, 2009). Een invloedrijke theorie die hieruit voortvloeide stelt dat we acties van anderen begrijpen door middel van interne motor simulatie (Iacoboni, Molnar-Szakacs, Gallese, Buccino, Mazziotta, & Rizzolatti, 2005; Rizzolati & Craighero, 2004; Rizolatti, Fogassi, & Gallese, 2001). Wanneer we fout observatie als een specifiek onderdeel van actie observatie bekijken, is het heel aanlokkelijk om te veronderstellen dat we ook elk anders fouten simuleren en dat we daarom dezelfde gebieden activeren bij fout observatie en fout executie. In **hoofdstuk vijf** hebben we deze predictie getest door hersen activiteit geassocieerd met de observatie van fouten die kunnen gesimuleerd worden te vergelijken met hersen activiteit van fouten die niet kunnen gesimuleerd worden. In het bijzonder hebben we hersen activatie gemeten terwijl proefpersonen dagelijkse mens-machine interacties waarnemen die resulteren in correcte of foute situaties. De reden voor deze fouten konden tweevoudig zijn. Ten eerste, kon de mens de fout veroorzaken door de machine verkeerd te gebruiken. Ten tweede, kon de fout veroorzaakt worden door een malfunctie van de machine. We toonden aan dat de pMPFC geen onderscheid maakte tussen fouten uitgelokt door mensen of door machines. Hiermee vonden we dus geen evidentie voor de simulatiehypothese. We vonden zelfs de meest uitgebreide activatie wanneer een niet foutieve onverwachte gebeurtenis op het scherm verscheen. Hiermee tonen onze data een bredere rol aan voor de pMPFC, namelijk het detecteren van opvallende gebeurtenissen.

Verder activeerde de observatie van menselijke fouten gebieden die betrokken zijn in visuele verwerking en actie begrip zoals de inferieure parietale kwab en de laterale occipitotemporale cortex. Dit reflecteert dat de observatie van menselijke fouten een versterkte activatie teweegbrengt in gebieden gerelateerd aan de visuele verwerking van lichaamsgerelateerde karakteristieken.

CONCLUSIE

In deze thesis toon ik aan dat resultaten verkregen in experimenteel onderzoek beïnvloed kunnen zijn door steeds dezelfde restrictieve set van paradigma’s te gebruiken. Ten eerste vinden we een dissociatie in de pMPFC wanneer fouten en conflict op een verschillend niveau worden gemeten. Ten tweede, tonen we aan dat de gedragseffecten die extensief beschreven werden in de literatuur verschillend zijn van deze gemeten in een meer ecologisch valide taak. Ten slotte tonen we aan dat de pMPFC niet alleen gerelateerd is aan de observatie van fouten maar ook aan de observatie van onverwachte verrassende gebeurtenissen. Samengevat, kunnen we concluderen dat adaptieve controle onderzocht moet worden op verschillende niveaus in een bredere range van taken en dat fout observatie onderzoek niet enkel moet focussen op menselijke fouten.

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