Cognitive demand and error feedback: fMRI evidence for individual differences of conflict monitoring in rostral versus dorsal ACC activity

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Abstract

Based on the conflict monitoring theory and the dual-mechanism of control account, we investigated individual differences (Trait-BIS, reasoning ability) of conflict monitoring depending on cognitive demand and aversive error feedback in the dorsal and rostral anterior cingulate cortex (dACC, rACC). We recorded fMRI data while participants ($n = 38$) performed an adapted go/nogo task with four balanced levels of cognitive demand (low vs. high) and error feedback (low aversive vs. high aversive). We observed more neural activity representing conflict monitoring intensity in dACC than rACC. Individuals with higher reasoning scores showed more intense conflict monitoring to nogo than go stimuli in dACC when cognitive demand was high. This finding suggests that individuals with higher reasoning scores invest conflict monitoring in a reactive manner to prevent errors when the task becomes more demanding. In contrast, individuals with higher Trait-BIS scores intensify their conflict monitoring in rACC even when cognitive demand is low and irrespective of stimulus type. Adaptation of conflict monitoring intensity in higher Trait-BIS individuals occurs in an anticipatory and less context-specific manner. Taken together, our results suggest that cognitive demand modulates individual differences of conflict monitoring and adjustment strategies of cognitive control.

Key words: ACC, reasoning, Trait-BIS, cognitive demand, error feedback

1. Introduction

Cognitive control (i.e., the protection and optimization of goal-directed behavior) is important for human behavior and several mechanisms are necessary for the control of cognition and action. Conflict monitoring has been discussed as one mechanism that indicates the need for control (e.g., when compatible and incompatible stimuli have to be discriminated). In the last years, the conflict monitoring model has inspired many studies which have shown that the Anterior Cingulate Cortex (ACC) is engaged in conflict monitoring and cognitive control (Botvinick, 2007; Botvinick, Cohen, & Carter, 2004; Brown, 2013). Based on the segregation model, the dorsal ACC (dACC, also known as caudal ACC or midcingulate cortex, MCC) has been related to cognitive processes, whereas the rostral ACC (rACC) has been related to the processing of emotional information and motivation (Bush, Luu, & Posner, 2000; Cavanagh & Shackman, 2015; Gray et al., 2005; Shackman et al., 2011; Shenhav, Botvinick, & Cohen, 2013). The integrative or adaptive model of ACC functioning presumes that cognitive control and affective processing (e.g., pain, negative affect) occur in the same region (e.g., Shackman et al., 2011; Shenhav et al., 2013). Thus, the segregation hypothesis would be confirmed when the dACC activity in a go/nogo task would be higher than the rACC activity because the differentiation of go and nogo stimuli in a go/nogo task should activate cognitive aspects of conflict monitoring. The integrative model of ACC functioning would be confirmed when dACC activity and rACC activity would not differ. By referring to most recent accounts on mechanisms of the cognition-motivation interaction (Botvinick & Braver, 2015; Braver et al., 2014; Cavanagh & Shackman, 2015; Shackman et al., 2011), the present study investigated the interplay of the dACC and the rACC as well as its relationship to individual differences of conflict monitoring and reactive vs. proactive adjustment of cognitive control.

Conflict monitoring, i.e., the intensity and frequency of conflict-signals, has been demonstrated to vary depending on cognitive demand (i.e., the working memory load that is needed to successfully perform a task) and feedback (Leue, Lange, & Beauducel, 2012; Leue, Weber, & Beauducel, 2014). Whereas cognitive demand manipulated by means of working memory load requires more intense cognitive processes of stimulus categorization during conflict monitoring, negative feedback following erroneous responses should be related to the

processing of motivational valence. EEG and behavioral studies (Kool & Botvinick, 2014; Leue et al., 2012; Leue et al., 2014) as well as fMRI studies (Hernandez Lallement et al., 2014; Vassena et al., 2014) have demonstrated that individuals adapt their ACC-related conflict monitoring intensity depending on cognitive demand and feedback. Thus, the investigation of the combined effects of cognitive demand and feedback on conflict monitoring facilitates our knowledge on how individuals recruit and adjust cognitive control (Braver, 2012; Braver, Gray, & Burgess, 2007; Weldon, Mushlin, Kim, & Sohn, 2013) and how they compensate inefficiency of information processing (e.g., Moser, Moran, Schroder, Donnellan, & Yeung, 2013). Therefore, the present study aimed at investigating how cognitive demand and error feedback modulate activity of the dACC and the rACC by using an a priori region of interest (ROI) approach based on coordinates published in a meta-analysis (Shackman et al., 2011).

Since many studies relate the dACC to cognitive demand (Shenhav, Cohen, & Botvinick, 2016), we expected the dACC relative to the rACC to be more activated in conditions with higher vs. lower cognitive demand. Shenhav et al. (2013; 2016) focus on the dACC and do not address an explicit role to the rACC. However, the evaluation of feedback as a basis for conflict monitoring might be affected by emotional states (e.g., anxiety). Since the rACC has been related to fear responding (Duval, Javanbakht, & Liberzon, 2015), we expected that the rACC may be activated especially when feedback is aversive. Accordingly, we expected the rACC relative to the dACC to be more activated in conditions with more vs. less aversive error feedback.

In accordance with prior studies (Burgess & Braver, 2010; Leue et al., 2012; Leue et al., 2014), we expected that individual differences of reasoning ability and anxiety-related traits modulate the adjustment of ACC-related conflict monitoring depending on cognitive demand and error feedback. Research on individual differences in working memory capacity has demonstrated that general fluid intelligence and reasoning ability are related to working memory capacity and the processing of task difficulty (Chudersky, 2013; Colom, Abad, Quiroga, Shih, & Flores-Mendoza, 2008; Colom, Rebello, Palacios, Juan-Espinosa, & Kyllonen, 2004; Engle, Tuholski, Laughlin, & Conway, 1999; Kyllonen & Christall, 1990;

Süß, Oberauer, Wittmann, Wilhelm, & Schulze, 2002). Moreover, the interference in working memory tasks was related to a stronger association of general fluid intelligence and activity of the prefrontal cortex (Burgess & Braver, 2010; Burgess, Gray, Conway, & Braver, 2011). Based on these findings it is likely that individual differences of general fluid intelligence and reasoning ability modulate conflict monitoring intensity.

Leue et al. (2014) investigated the relation between reasoning ability and working memory capacity. Reasoning ability is a core determinant of intelligence that is related to verbal, numerical, and figural abilities, whereas general fluid intelligence has been described as the ability to solve problems, to recognize patterns, and to learn (Cattell, 1971). It has also been shown that verbal and numerical abilities are relevant for information processing that requires working memory capacity (Colom et al., 2004; Süß et al., 2002). To integrate verbal, numerical, and figural aspects of reasoning we subsequently use the term “total reasoning”. Leue et al. (2014) observed that total reasoning and more precisely figural ability are directly related to conflict monitoring especially in conditions with more aversive error feedback (i.e., monetary loss following erroneous responses). Thus, individuals with higher total reasoning scores used error feedback in order to adapt their conflict monitoring intensity. The fact that error feedback instead of cognitive demand was used as a teaching signal for the adaptation of conflict monitoring intensity suggests that individuals with higher vs. lower total reasoning ability use previous emotionally aversive information to prevent error feedback in future. This tendency of individuals with higher total reasoning ability to learn from aversive events in the past in order to prevent aversive events in the future should go along with a stronger increase of conflict monitoring intensity in rACC compared to dACC. Leue et al. (2014) have shown that individuals with higher total reasoning ability adapt their conflict monitoring intensity in a reactive manner. In accordance with Braver’s (2012) dual mechanisms of control approach, reactive control means that goal representations are activated only when they are needed. To this end, reactive control is highly efficient but reactive control needs external trigger such as error feedback to reactivate task goals (e.g., aiming to respond more correctly after an error). In accordance with Leue et al. (2014), we expected individuals with higher total reasoning

ability to use more intense reactive cognitive control to reactivate task goals (e.g., correct performance after errors) than individuals with lower total reasoning ability.

Proactive control is triggered in advance to the implementation of goals. When no errors are committed this might be due to a sustainable successful proactive control. Thus, no or a small number of errors (e.g., one error per task block) might be due to a more pronounced tendency of proactive control. Because errors are highly aversive to higher anxious individuals, they might favor a less efficient, proactive style of cognitive control compared to lower anxious individuals in order to prevent errors. More proactive control in higher vs. lower anxious individuals is likely to be associated with higher dACC activity compared to rACC activity (cf. Braver et al., 2012). If proactive control was unsuccessful and errors occurred, these errors serve as a trigger to reactivate cognitive control. Prior research has demonstrated that less aversive feedback is sufficient in order to intensify conflict monitoring in higher anxious individuals (Leue, Cano Rodilla, & Beauducel, 2017; Leue et al., 2012; Leue et al., 2014). Less is known about the role of cognitive demand, processing of error feedback and reactive control for dACC and rACC activity of higher vs. lower anxious individuals. Two predictions are possible: With regard to the segregation hypothesis, more aversive error feedback might be expected to intensify rACC activity in higher vs. lower anxious individuals. From the perspective of proactive control, more intense dACC activity in higher vs. lower anxious individuals cannot be ruled out as a tool of error prevention. Thus, to learn more about the ACC functioning in higher vs. lower anxious individuals in conditions of balanced error feedback and cognitive demand, we investigated the modulating role of these determinants for dACC and rACC functioning.

Altogether our hypotheses were as follows (Figure 1): Withholding predominant responses should require more intense conflict monitoring and control processes in dACC-regions. Therefore, we expected a more intense dACC-related conflict monitoring following nogo stimuli compared to go stimuli (hypothesis 1). With regard to cognitive demand, we presumed that higher compared to lower cognitive demand results in a more intense conflict monitoring in dACC (hypothesis 2). Regarding error feedback (hypothesis 3), we expected the rACC activity during processing of go and nogo stimuli to be more pronounced in

conditions that result in more aversive error feedback (i.e., monetary loss following errors) when errors occur compared to conditions with less aversive error feedback (i.e., verbal error feedback). In accordance with Leue et al. (2014), individuals with higher total reasoning ability can be expected to intensify their conflict monitoring and subsequently their reactive cognitive control to reactivate task goals when tasks comprise error feedback. Therefore, we expected that individuals with higher vs. lower total reasoning scores show an increase in conflict monitoring in rACC in conditions with higher compared to lower cognitive demand (hypothesis 4). Leue et al. (2014) demonstrated for the nogo N2 amplitude (whose generator lies in the ACC) that cognitive demand can overrule reinforcement effects during conflict monitoring. As cognitive demand and error feedback conditions were the same as in Leue et al. (2014), we predicted individuals with higher vs. lower trait-BIS scores to show a more pronounced dACC activity (more proactive control) in conditions with more aversive vs. less aversive error feedback (hypothesis 5).

----Please insert Figure 1 about here----

Method

Participants

The present study investigated $N = 43$ participants (22 male). Five participants were excluded because of technical problems during data acquisition. A total of $N = 38$ participants (18 male) was available for statistical analysis (mean age: $M = 26.00$ years, $SD = 7.28$, range: 19-49 years). As indicated by the Edinburgh Handedness Inventory (Oldfield, 1971), all participants were right-handed. Participants had normal or corrected-to-normal vision. All participants declared that they had never suffered from a neurological disease or any other diseases. The study was approved by the ethics committee of the Medical Faculty, University of Bonn, Germany.

Measures

Participants filled in the German version of the BIS/BAS scales (Strobel, Beauducel, Debener, & Brocke, 2001) that was originally published by Carver and White (1994). The BIS/BAS

scales comprise 7 trait-BIS and 13 trait-BAS items. All items are answered on a 4-point Likert scale (“1” indicating strong disagreement and “4” indicating strong agreement). The trait-BIS scale measures an individuals’ sensitivity to aversiveness and has been applied in studies investigating individual differences of conflict monitoring. The trait-BAS scale measures an individuals’ sensitivity to appetitive stimuli such as reward or relief of punishment. In the present study, the trait-BIS scale and the trait-BAS scale demonstrated a moderate reliability similar to prior studies (Leue et al., 2014). Reasoning ability was assessed with the German version of the basic module of the Intelligence-Structure-Test 2000 R (form A, Beauducel, Liepmann, Horn, & Brocke, 2010; Liepmann, Beauducel, Brocke, & Amthauer, 2007). Verbal ability was assessed with a verbal analogy task (items 21-40), numerical ability was assessed with a numerical calculation task (items 61-80), and figural ability was examined with a figural matrices task (items 161-180). Based on these three tasks a reasoning sum score was computed.

Go/nogo task

The present go/nogo task is an adaption of the task applied in Leue et al. (2014). The go/nogo task was programmed by using Python software (version 3.3.3.). Adaptation refers to trial timing so that the task was suitable for the recording of fMRI data. Number of stimuli per condition was reduced from 250 to 100 stimuli per task condition. As in Leue et al. (2014), go and nogo stimuli occurred with an 80:20 ratio in each of the four task blocks. Among ten trials there were always two nogo stimuli presented but never more than three nogo trials followed in a direct sequence. Go and nogo stimuli were geometric forms of either a square or a circle. Each task condition incorporated the combination of a cognitive demand level (low vs. high) and an error feedback level (low vs. high). Block A represented a combination of low cognitive demand and low error feedback, Block B included a combination of high cognitive demand and low error feedback, Block C incorporated low demand and high error feedback, and Block D combined high cognitive demand and high error feedback. Cognitive demand was manipulated by working memory load. In low demand conditions participants were asked to respond to a white colored geometric form (circle or square) and to withhold

responses when the other geometric form occurred. In the high cognitive demand condition participants were asked to respond to one pre-defined colored go stimulus (e.g., brown colored circle) and to withhold their responses to three different colored geometric forms (e.g., blue colored circle or square and brown colored square). Conditions including one white colored geometric form as a go and a nogo stimulus, respectively, were thought to represent low cognitive demand, because participants had to keep in mind only one go and one nogo stimulus. In the high cognitive demand condition participants had to keep in mind one colored go geometric form and three different nogo stimuli of the same form or color as the go stimulus which should require more cognitive demand. In case of erroneous responses, two task conditions provided low error feedback on trial and the other two task conditions included high error feedback on trial. Less aversive error feedback was represented by means of verbal error feedback (e.g., Error! or Too slow!) and more aversive error feedback was a verbal and monetary loss feedback (e.g., Error: -3 Ct! or Too slow: -3 Ct!). In case of correct responses, we provided the trial-by-trial feedback “Saved!”.

The four task conditions were presented in a pseudorandom order (ABCD, BCDA, CDAB, or DABC). Participants were randomly assigned to one sequence of task conditions. Conditions ABCD and DABC included each nine participants with men and women being (widely) equal probably assigned to each task condition. Conditions BCDA and CDAB included each ten participants with men and women again being equal probably assigned to each task condition. Each trial sequence comprised a fixation cross (1000 ms), a go or a nogo stimulus (100 ms), a response interval (≤ 500 ms), a variable time interval (3000-5000 ms), a feedback (1000 ms), and a variable inter-trial interval (3000-5000 ms). Figures 2 A to D represent examples of trial sequences.

----Please insert Figure 2 about here----

Procedure

Participants were recruited through announcements on bulletin boards and electronic platforms. Participants who were interested in this study were instructed by email to omit alcohol use, to avoid unusual caffeine consumption, and to avoid taking any medication the

day before fMRI recording. The standard Cambridge exclusion criteria for fMRI studies were followed (Bishop, Duncan, Brett, & Lawrence, 2004, no metal, no history of neurological disease, no head injury). Further exclusion criteria were pregnancy, claustrophobia, age < 18 years, psychiatric diseases, and impaired physiological health. Participants were not allowed to wear any metal objects in the scanner.

At the beginning of each examination participants were informed about content and duration of the examination. All participants gave written informed consent. Participants filled in personality questionnaires and they rated their current affect by means of the self-assessment manikin (SAM, Bradley and Lang, 1994) before they were placed in the scanner and after leaving the scanner. The day before scanning participants performed three tasks of the intelligence-structure-test, module A (Beauducel et al., 2010; Liepmann et al., 2007). Task performance took about 20 minutes per task block. A 2-minutes break was given after each task block. Participants received a payment of 30 Euros.

fMRI acquisition and pre-processing

Scanning was performed on a 1.5-T Avanto Scanner (Siemens, Erlangen, Germany) using an 8-channel head coil. Functional data were acquired using an Echo Planar Imaging (EPI) sequence with a repetition time (TR) of 2.5s, an echo time (TE) of 45 ms and a flip angle of 90 degrees. Each volume comprised 31 axially acquired slices in ascending order with no gap between slices (field of view: 192 mm, data matrix: 64 x 64, in-plane voxel resolution: 3 x 3 mm). A high-resolution T1-weighted MRI MPRAGE scan (TR: 1660 ms, TE: 3.089 ms, data matrix: 256 x 256, number of slices: 160, voxel resolution: 1 x 1 x 1 mm) was acquired for each participant to inform structure-function mapping. The experiment was presented by Presentation® software version 14.9 (Neurobehavioral Systems, USA) via video goggles (Nordic Neuro Lab, Norway) and subjects gave their answer by button presses on MRI-suited response grips (Nordic Neuro Lab). fMRI data were pre-processed using Statistical Parametric Mapping software (SPM12, <http://www.fil.ion.ucl.ac.uk/spm>) based on Matlab R2016a. The ~1840 volumes/scans were realigned to the first volume in the first run, re-sliced using sinc interpolation (SPM12, “Realign”), and slice time corrected to account for

differences in slice acquisition time (SPM12, “Slice timing”); the structural scan of each participant was co-registered to the mean functional scan (SPM12, “Coregister”) and segmented into grey and white matter and cerebro-spinal fluid (SPM12, “Segment”) to derive linear transformations to standardized stereotaxic MNI space that were then applied to the EPIs and to the structural scan (SPM12, “Normalize: Write”). Finally, the EPIs were spatially smoothed to improve the signal-to-noise ratio using an isotropic 8 mm full-width at half-maximum (FWHM) Gaussian kernel (SPM12, “Smooth”).

The design matrix for each participant consisted of 5 experimental regressors per run. These corresponded to correct Go trials, correct Nogo trials, combined incorrect Go and incorrect Nogo trials, error feedback, and fixation; they were derived by convolving the stimulus response function to each brief event with SPM’s canonical hemodynamic response function. Depending on the task block, Go trials were high-demand, low-error feedback Go trials, high-demand, high-error feedback Go trials, low-demand, low-error feedback Go trials, or low-demand, high-error feedback Go trials; the same applied to the other regressors. Data were high-pass filtered at 1/128 Hz to remove slow drifts in the signal. We extracted the BOLD signal (beta weights) for each regressor in anatomically defined ROIs using MarsBaR (Brett, Anton, Valabregue, & Poline, 2002). We interpret more positive beta weights as an operationalization of more intense conflict monitoring because the BOLD signal was extracted stimulus-locked (i.e., following go and nogo stimuli). The ROIs were spherical ROIs with a radius of 15 mm (volume: 14400, based on coordinates reported in Gray et al. (2005) and Shackman et al. (2011), for rostral ACC [0, 43, 12] and dorsal ACC [0, 10, 46], respectively (Figure 3).

----Please insert Figure 3 about here----

Statistical analysis

Behavioral data were analyzed using SPSS 23. A repeated measures ANCOVA was performed for the percentage of correct responses including Stimulus type (go vs. nogo stimulus), Cognitive demand (low vs. high), and Error feedback (low aversive: verbal error feedback vs. high aversive: verbal error feedback combined with monetary loss) as repeated

measures factors. Gender and Block sequence were inserted as between-subjects factors. A second repeated measures ANCOVA for correct go response times included Cognitive demand (low vs. high) and Error feedback (low aversive vs. high aversive) as repeated measures factors. Sensitivity d' was computed according to Stanislaw and Todorov (1999). The third repeated measures ANCOVA was performed to analyze feedback ratings and affect ratings. For the fMRI data, the fourth repeated measures ANCOVA incorporated ACC-region (dACC vs. rACC), Stimulus type (Go vs. Nogo), Cognitive demand (low vs. high), and Error feedback (verbal vs. monetary) as repeated measures factors.

Mean centered Total reasoning scale scores and Trait-BIS scale scores were entered as covariates (i.e., as continuous variables to avoid variance reduction) in all repeated measures ANCOVAs. Because all repeated measures factors included no more than two levels, Greenhouse-Geisser correction did not apply as a correction for sphericity violation. We report η_p^2 to indicate the effect sizes of main effects or interactions. Response times were normally distributed (Shapiro-Wilk test: $ps > .10$).

Results

Correlations between personality and reasoning ability

Table 1 shows that Trait-BIS and Total reasoning ability were moderately reliable. Trait-BIS did not significantly correlate with Total reasoning. These findings suggest that the scales measure individual differences on independent constructs.

----Please insert Table 1 about here----

Percentage of correct responses

Percentage of correct responses revealed a significant Stimulus type main effect, $F(1,28) = 28.47$, $p < .01$, $\eta_p^2 = .50$. The percentage of correct responses was higher for go stimuli compared to nogo stimuli (Table 2) suggesting that conflict monitoring and inhibition of the pre-potent responses was less successful for nogo stimuli. That is, the pre-potent responses were more difficult to inhibit for nogo compared to go stimuli. No further main effects or

interactions including Stimulus type, Error feedback, Cognitive demand or the trait dimensions were significant, $F_s < 3.60$, ns.

Response times

A significant Cognitive demand main effect was observed for correct go responses, $F(1,28) = 18.00$, $p < .01$, $\eta_p^2 = .39$. Correct response times to go stimuli were faster for low demand than high demand (Table 2). No further main effects or interactions including Stimulus type, Error feedback, Cognitive demand or the trait dimensions were significant, $F_s < 1.60$, ns.

Sensitivity d'

For sensitivity d' , exclusively the Cognitive demand main effect was significant, $F(1,28) = 6.80$, $p < .05$, $\eta_p^2 = .20$. Sensitivity d' was larger in high cognitive demand conditions compared to low cognitive demand conditions (Table 2). No further main effects or interactions including Stimulus type, Error feedback, Cognitive demand or the trait dimensions were significant, $F_s < 5.15$, ns.

---- Please insert Table 2 about here ----

Feedback and affect ratings

The ANCOVA of unpleasantness ratings (1 = less unpleasant, 9 = highly unpleasant, available for $n = 28$, 13 female) revealed a significant main effect for Type of feedback, $F(2,34) = 34.49$, $p < .01$, $\eta_p^2 = .67$. Neutral “saved!” feedback was rated as less unpleasant ($M = 1.70$, $SE = 0.23$) than verbal error feedback ($M = 5.04$, $SE = 0.30$), $F(1,17) = 75.94$, $p < .01$, $\eta_p^2 = .82$, and monetary loss feedback ($M = 5.31$, $SE = 0.49$), $F(1,17) = 30.99$, $p < .01$, $\eta_p^2 = .65$. Unpleasantness ratings of verbal error feedback and monetary feedback did not significantly differ, $F(1,17) = 0.28$, $p = .60$.

State-affect ratings revealed a main effect of Pleasantness, $F(1,28) = 131.80$, $p < .01$, $\eta_p^2 = .83$, with pre-rating ($M = 2.95$, $SE = 0.21$) showing lower Pleasantness scores than post-rating ($M = 6.54$, $SE = 0.20$). Moreover, a Pleasantness $\times$ Trait-BIS interaction was observed, $F(1,28) = 11.43$, $p < .01$, $\eta_p^2 = .29$. Partial correlation (controlling for gender and block

sequence) between Trait-BIS and pre-Pleasantness ratings indicated that individuals with higher Trait-BIS scores just tended to describe higher pre-Pleasantness ratings (partial $r(34) = .32, p = .06$), whereas the partial correlation between Trait-BIS scores and post-Pleasantness ratings indicated significantly higher post-Pleasantness in individuals with higher Trait-BIS scores (partial $r(34) = .39, p < .05$). That is, individuals with higher Trait-BIS scores reported more pleasantness after task performance. We found a main effect for State-excited ratings, $F(1,28) = 26.76, p < .01, \eta_p^2 = .49$. Pre-state excited ratings were lower ($M = 4.25, SE = 0.14$) than Post-state excited ratings ($M = 5.24, SE = 0.19$).

fMRI data

fMRI results with regard to a priori hypotheses

Repeated measures ANCOVA revealed a significant ACC-region $\times$ Stimulus type interaction, $F(1,28) = 4.39, p < .05, \eta_p^2 = .14$ (hypothesis 1, Figure 4 A). Beta weights were more positive for nogo stimuli ($M = 0.94, SE = 0.19$) than for go stimuli in rACC ($M = 0.66, SE = 0.16$), $F(1,28) = 6.72, p < .05, \eta_p^2 = .15$, but not in dACC, $F(1,28) < 1$, ns. The ACC-region $\times$ Cognitive demand interaction was not significant, $F(1,28) < 1$, ns (hypothesis 2). The ACC-region $\times$ Error feedback interaction was not significant, $F(1,28) < 1$, ns (hypothesis 3). The ACC-region $\times$ Cognitive demand $\times$ Total reasoning interaction was not significant, $F(1,28) < 1$, ns (hypothesis 4). The ACC-region $\times$ Error feedback $\times$ Trait-BIS interaction was not significant, $F(1,28) < 1$, ns (hypothesis 5). Table 3 summarizes the results for our a priori hypotheses.

Since the dependent variables for these ANCOVAs were based on rather large 15 mm spherical ROIs without movement correction, we also performed the respective ANCOVAs for dependent variables based on 15mm spherical ROIs with movement correction, for 10mm spherical ROIs with movement correction and without movement correction, and for ROIs based on the Mindboggle-101 dataset (Klein & Tourville, 2012) with movement correction (see Supplement, Table S1). The ACC-region $\times$ Stimulus type interaction with more positive beta weights for nogo stimuli (hypothesis 1) was significant for all spherical ROI analyses, but not for the analysis based on the Mindboggle-101 dataset and tended to be significant for

the 15 mm spherical ROIs with movement correction. As for the ANCOVAs based on the initial ROI, the hypotheses 2 to 5 were all not confirmed for these additional analyses.

---- Please insert Table 3 about here ----

Additional fMRI results

In accordance with the segregation hypothesis, the ACC-region main effect was significant and robust across all analyses (Table S1), $F(1,28) = 8.17$, $p < .01$, $\eta_p^2 = .23$, with dACC vs. baseline activity ($M = 1.27$ beta weights, $SE = 0.24$) being more pronounced compared to rACC vs. baseline activity ($M = 0.75$ beta weights, $SE = 0.18$, Figure 4 B). Additional significant results that do not directly confirm our a priori hypotheses are also summarized in Table 3. The ACC-region $\times$ Stimulus type $\times$ Error feedback interaction was significant and robust across all analyses except Mindboggle (Table S1), $F(1,28) = 7.76$, $p < .01$, $\eta_p^2 = .22$, and could be traced back to an ACC-region $\times$ Stimulus type interaction in conditions with less aversive error feedback, $F(1,28) = 12.68$, $p < .01$, $\eta_p^2 = .31$ (for high aversive error feedback: ACC-region $\times$ Stimulus type interaction, $F < 1$, ns). The ACC-region $\times$ Stimulus type interaction in conditions with less aversive error feedback could be traced back to a significant ACC-region main effect for Go stimuli (robust across all analyses Table S1), $F(1,28) = 17.62$, $p < .01$, $\eta_p^2 = .39$, with dACC activity relative to baseline activity ($M = 1.25$ beta weights, $SE = 0.24$ beta weights) being more pronounced compared to rACC activity relative to baseline activity for Go stimuli ($M = 0.66$ beta weights, $SE = 0.16$). This finding indicates that the monitoring for predominant go responses has been more strongly innervated by dACC rather than by rACC.

The ACC-region $\times$ Stimulus type $\times$ Cognitive demand $\times$ Total reasoning interaction was significant exclusively for the 15 mm spherical ROIs without movement correction (cf. Table S1), $F(1,28) = 5.07$, $p < .01$, $\eta_p^2 = .15$. In dACC, the Stimulus type $\times$ Cognitive demand $\times$ Total reasoning interaction was significant (across all analyses Table S1), $F(1,28) = 11.29$, $p < .01$, $\eta_p^2 = .29$, but not in rACC, $F(1,28) = 1.82$, $p = .19$. For low cognitive demand, we observed a tendency of a Stimulus type $\times$ Total reasoning interaction in dACC exclusively for the 15 mm spherical ROIs without movement correction (cf. Table S1), $F(1,28) = 4.15$, $p =$

.05, $\eta_p^2 = .13$. For high cognitive demand, the Stimulus type $\times$ Total reasoning interaction in dACC was significant and robust across all analyses except Mindboggle (Table S1), $F(1,28) = 4.56$, $p < .05$, $\eta_p^2 = .14$. Individuals with higher reasoning scores showed more pronounced activity to Nogo relative to Go stimuli in dACC in high cognitive demand conditions (Figure 4 C). This finding suggests that individuals with higher reasoning scores demonstrate more intense monitoring to Nogo stimuli compared to Go stimuli when cognitive demand is high. That is, individuals with higher reasoning ability are more likely to (reactively) invest more conflict monitoring in order to successfully control behavior (i.e., inhibit responses to nogo stimuli) when cognitive demand is high. The ACC-region $\times$ Cognitive demand $\times$ Total reasoning interaction was not significant, $F(1,28) < 1$, ns.

---Please insert Figure 4 A to D about here---

Finally, the ACC-region $\times$ Cognitive demand $\times$ Trait-BIS interaction was significant for the 15 mm and 10 mm spherical ROIs without movement correction (Table S1), $F(1,28) = 7.17$, $p < .05$, $\eta_p^2 = .20$. This three-way interaction could be traced back to a significant Cognitive demand $\times$ Trait-BIS interaction in rACC, which was also significant for the 15 mm spherical ROIs with movement correction and the 10 mm spherical ROIs without movement correction (Table S1), $F(1,28) = 4.35$, $p < .05$, $\eta_p^2 = .13$, but not in dACC, $F(1,28) < 1$, ns. This interaction suggested that individuals with higher Trait-BIS scores revealed a more pronounced rACC activity than individuals with lower Trait-BIS scores exclusively in conditions with low cognitive demand (Figure 4 D).

As indicated in Table 3 (bottom) we did not observe evidence for the integrative hypothesis. Evidence for the integrative hypothesis would mean that effects of cognitive demand, error feedback, and interactions of cognitive demand and error feedback with individual differences occur in ACC without separation in dACC and rACC functioning, $F_s(1,28) < 1$, ns.

Discussion

The present study investigated cognitive control related to dACC and rACC activity in a go/nogo task with balanced conditions of error feedback and cognitive demand. Contrary to hypothesis 1, the more intense conflict monitoring to nogo stimuli compared to go stimuli was observed in rACC instead of dACC. This finding suggests evidence for the integrative hypothesis because participants did obviously not solely process the cognitive content of the nogo stimuli but processed affective content associated with nogo stimuli (e.g., anticipation of errors and aversive feedback following errors). Hypotheses 2 to 5 were not confirmed because the expected interactions were not significant (Table 3). Even when the dependent variables were based on different ROIs with movement correction and without movement correction hypotheses 2 to 5 were not confirmed.

Moreover, we observed other (not a priori predicted) significant fMRI results which are discussed with post-hoc explanations. The more intense conflict monitoring in dACC relative to rACC corresponds to the segregation hypothesis. The fact that the dACC was more activated than the rACC in a go/nogo task suggests that stimulus type (nogo vs. go) serves as a teaching signal (Botvinick, 2007) for the intensification of conflict monitoring. To this end, dACC activity basically works to prevent errors. Thus, the results extend prior predictions assuming that the dACC monitors for cognitive costs and task difficulty (Botvinick et al., 2004; Botvinick, Huffstetler, & McGuire, 2009; Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004). In a cost-benefit analysis, the benefits of cognitive control are weighed against its drawbacks (Botvinick & Braver, 2015, p. 92). However, task difficulty and cognitive demand can also be inferred from feedback. The current expected value of control model (Shenhav et al., 2016) refers to feedback as a parameter that triggers the intensity of conflict monitoring. According to more integrative accounts of ACC functioning, the more intense dACC activity following go stimuli in conditions with less aversive error feedback (i.e., verbal error feedback) illustrates that early stages of conflict monitoring are obviously not independent of the affective (anticipated) stimulus meaning (e.g., anticipation of potential aversive feedback). When error feedback is less intense, the dACC provides more intense conflict monitoring to go responses probably in order to prevent errors at all or to prevent

further errors (Spearman's Rho for dACC activity in conditions with high demand and low error feedback with number of omission errors collapsed across task conditions: $-.31, p = .06$). Thus, the dACC seems to innervate cognitive control in an anticipatory manner by means of intensifying conflict monitoring. However, the non-confirmation of the more intense rACC activation in conditions involving more aversive error feedback could also be due to a rather low intensity of the aversive feedback (i.e., losing 3 Ct). Larger monetary loss may induce more intense emotional processing.

Individuals with higher vs. lower reasoning scores invested more conflict monitoring in dACC to nogo stimuli and when cognitive demand was high. This finding (which was robust across all analyses exclusively Mindboggle) suggests that individuals with higher reasoning scores adjust their conflict monitoring intensity more trigger-specific, in a reactive manner (Braver, 2012). The present results indicate that individuals with higher reasoning ability may be more prepared for adjusting cognitive control when the tasks are challenging (i.e., on trigger-specific demands; Weldon et al., 2013; Leue et al., 2014). In contrast, individuals with higher anxiety-related traits showed a more intense rACC activity in low demand conditions than individuals with lower anxiety-related traits. This finding suggests that the anticipation of errors motivates more intense conflict monitoring irrespective of feedback intensity, stimulus type, and even when cognitive demand is low. As this result was robust exclusively for the 15 mm spherical ROIs with movement correction and the 10 mm spherical ROIs without movement correction we interpret this result with caution: This processing style might indicate a form of proactive control in individuals with higher anxiety-related traits (Braver, 2012). It is noteworthy that the recruitment of cognitive control already starts in situations with low cognitive demand, although response adaptation in terms of slower reaction times (RTs) to Go stimuli has been observed in situations with high cognitive demand. Slower RTs have been described as a consequence of performance costs that are induced in conflict situations (Botvinick & Cohen, 2014, S. 1257). Our data suggest that response adaptation in terms of slower RTs in high demand conditions is observed when the recruitment of cognitive control that is already observed in low demand conditions is not sufficient. These findings extend the study of Leue et al. (2014), who demonstrated an

intensified conflict monitoring (by means of the N2 event-related potential in an EEG paradigm) and slower RTs to Go stimuli in high cognitive demand conditions. As conflict monitoring and cognitive control are reciprocally related (Botvinick, Nystrom, Fissell, Carter, & Cohen, 1999; Kerns et al., 2004), one might presume the following sequence of monitoring, cognitive control and behavioral adjustment: As long as an intensified cognitive control is sufficient to successfully perform a task (e.g., low demand conditions), performance adaptation and intensification of conflict monitoring are not immediately necessary. When task requirements become more intense (e.g., in high demand conditions), individuals intensify their conflict monitoring, they increase their sensitivity d' in order to discriminate information and/or they slow down their responses. Both tendencies might function to obtain further information and to successfully perform tasks.

Because we did not observe an interaction of cognitive demand $\times$ error feedback, future research might demonstrate evidence on the adjustment of conflict monitoring and cognitive control depending on cognitive demand, feedback, and individual differences in an fMRI experiment. Recent research has outlined mechanisms of the motivation-cognition interaction (Braver et al., 2014) that might serve as a promising theoretical basis in order to further our understanding on individual differences of conflict monitoring and cognitive control. Our analysis of the fMRI data focused on a priori ROIs that were derived from meta-analytic findings on ACC functioning. In order to elucidate and differentiate the functioning of further brain regions (e.g., ACC, MCC, posterior cingulate cortex, Leech & Sharp, 2014) involved in the motivation-cognition interaction beyond dACC and rACC functioning whole brain analyses or functional connectivity analyses are promising (Botvinick & Braver, 2015).

Conclusion

In a go/nogo task with balanced levels of cognitive demand and aversive error feedback, we demonstrate evidence for the segregation hypothesis and for the integrative hypothesis of differential ACC functioning. We demonstrate that stimulus type served as a teaching signal for conflict monitoring in rACC, whereas cognitive demand served as a teaching signal for conflict monitoring in dACC. Based on the interaction of cognitive demand and individual differences, we demonstrate that

the integration of Botvinick's conflict monitoring framework and Braver's dual mechanism of control accounts for differential ACC functioning. Individuals with higher total reasoning scores adjust their conflict monitoring intensity in a more reactive manner (i.e., when cognitive demand is high and nogo stimuli indicate a more intense conflict signal) than individuals with lower total reasoning scores. Individuals with higher trait-BIS scores adjust their conflict monitoring intensity in a more proactive manner (i.e., even when cognitive demand is low and irrespective of the intensity of conflict signal) than individuals with lower trait-BIS scores. Taken together, we present for the first time that total reasoning ability and trait anxiety are related to different strategies of adjusting cognitive control in ACC depending on context factors. We also present robust findings across different analyses for the experimental results including cognitive demand and error feedback of differential ACC activity. Differential ACC activity for total reasoning was robust across all analyses except Mindboggle and for trait-anxiety across ROI size and with vs. without movement correction.

Conflict of interest statement

The authors declare that they have no conflict of interest.

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References

- Beauducel, A., Liepmann, D., Horn, S., & Brocke, B. (2010). *Intelligence-Structure-Test English version of the Intelligenz-Struktur-Test 2000 R (I-S-T 2000 R)*. Göttingen: Hogrefe.
- Bishop, S., Duncan, J., Brett, M., & Lawrence, A. D. (2004). Prefrontal cortical function and anxiety: controlling attention to threat-related stimuli. *Nature Neuroscience*, 7, 184-188.
- Botvinick, M. M. (2007). Conflict monitoring and decision making: Reconciling two perspectives on anterior cingulate function. *Cognitive, Affective, and Behavioral Neuroscience*, 7, 356-366.
- Botvinick, M. M., & Braver, T. S. (2015). Motivation and cognitive control: From behavior to neural mechanism. *Annual Review of Psychology*, 66, 83-113.
- Botvinick, M. M., & Cohen, J. D. (2014). The computational and neural basis of cognitive control: Charted territory and new frontiers. *Cognitive Science*, 38, 1249–1285.
- Botvinick, M. M., Cohen, J. D., & Carter, C. S. (2004). Conflict monitoring and anterior cingulate cortex: An update. *Trends in Cognitive Science*, 8, 539-546.
- Botvinick, M. M., Huffstetler, S., & McGuire, J. T. (2009). Effort discounting in human nucleus accumbens. *Cognitive, Affective and Behavioral Neuroscience*, 9, 16-27.
- Botvinick, M. M., Nystrom, L. E., Fissell, K., Carter, C. S., & Cohen, J. D. (1999). Conflict monitoring versus selection-for-action in anterior cingulate cortex. *Nature*, 402, 179-181.
- Braver, T. S. (2012). The variable nature of cognitive control: a dual mechanisms framework. *Trends in Cognitive Sciences*, 16, 106-113.
- Braver, T. S., Gray, J. R., & Burgess, G. C. (2007). Explaining the many varieties of working memory variations: Dual mechanisms of cognitive control. In A. R. A. Conway, A. Miyake, C. Jarrold, J. Towse, & M. J. Kane (Eds.), *Variation in working memory* (pp. 76-106). Oxford: University Press.

- Braver, T. S., Krug, M. K., Chiew, K. S., Kool, W., Westbrook, J. A., Clement, N. J., . . . Somerville, L. H. (2014). Mechanisms of motivation–cognition interaction: challenges and opportunities. *Cognitive, Affective and Behavioral Neuroscience*, 14, 443-472. doi:10.3758/s13415-014-0300-0
- Brett, M., Anton, J.-L., Valabregue, R., & Poline, J. B. (2002). Region of interest analysis using an SPM toolbox (abstract). *Neuroimage*, 16 (suppl. 2).
- Brown, J. W. (2013). Beyond conflict monitoring: Cognitive control and the neural basis of thinking before you act. *Current directions in psychological science*, 22, 179-185.
- Burgess, G. C., & Braver, T. S. (2010). Neural mechanisms of interference control in working memory: Effects of interference expectancy and fluid intelligence. *Plos one*, 5(9), e12861.
- Burgess, G. C., Gray, J. R., Conway, A. R. A., & Braver, T. S. (2011). Neural Mmechanisms of interference control underlie the relationship between fluid intelligence and working memory span. *Journal of Experimental Psychology: General*, 140, 674-692.
- Bush, G., Luu, P., & Posner, M. (2000). Cognitive and emotional influences in anterior cingulate cortex. *Trends in Cognitive Sciences*, 4, 215-222.
- Carver, C. S., & White, T. L. (1994). Behavioral inhibition, behavioral activation, and affective responses to impending reward and punishment: The BIS/BAS scales. *Journal of Personality and Social Psychology*, 67, 319-333.
- Cattell, R. B. (1971). *Abilities: Their structure, growth, and action*. New York: Houghton Mifflin.
- Cavanagh, J. F., & Shackman, A. J. (2015). Frontal midline theta reflects anxiety and cognitive control: Meta-analytic evidence. *Journal of Physiology - Paris*, 109, 3-15.
- Chudersky, A. (2013). When are fluid intelligence and working memory isomorphic and when are they not? *Intelligence*, 41, 244-262.
- Colom, R., Abad, F. J., Quiroga, M. A., Shih, P. C., & Flores-Mendoza, C. (2008). Working memory and intelligence are highly related constructs, but why? *Intelligence*, 36, 584-606.

- Colom, R., Rebello, I., Palacios, A., Juan-Espinosa, M., & Kyllonen, P. C. (2004). Working memory is (almost) perfectly predicted by g. *Intelligence*, 32, 277-296.
- Duval, E. R., Javanbakht, A., & Liberzon, I. (2015). Neural circuits in anxiety and stress disorders: a focused review. *Therapeutics and Clinical Risk Management*, 11, 115–126.
- Engle, R. W., Tuholski, S. W., Laughlin, J. E., & Conway, A. R. A. (1999). Working memory, short-term memory, and general fluid intelligence: A latent variable approach. *Journal of Experimental Psychology: General*, 128, 309-331.
- Gray, J. R., Burgess, G. C., Schaefer, A., Yarkoni, T., Larsen, R. L., & Braver, T. S. (2005). Affective personality differences in neural processing efficiency confirmed using fMRI. *Cognitive, Affective and Behavioral Neuroscience*, 5, 182-190.
- Hernandez Lallement, J., Kuss, K., Trautner, P., Weber, B., Falk, A., & Fließbach, K. (2014). Effort increases sensitivity to reward and loss magnitude in the human brain. *Social Cognitive and Affective Neuroscience*, 9, 342-349.
- Kerns, J. G., Cohen, J. D., MacDonald, A. W., Cho, R. Y., Stenger, V. A., & Carter, C. S. (2004). Anterior cingulate conflict monitoring and adjustments in control. *Science*, 303, 1023-1026.
- Klein, A., & Tourville, J. (2012). 101 labeled brain images and a consistent human cortical labeling protocol. *Frontiers in Neuroscience*, Article 171.
- Kool, W., & Botvinick, M. M. (2014). A labor/leisure tradeoff in cognitive control. *Journal of Experimental Psychology: General*, 143, 131–141.
- Kyllonen, P. C., & Christall, R. E. (1990). Reasoning ability is (little more than) working memory capacity?! *Intelligence*, 14, 389-433.
- Leue, A., Cano Rodilla, C., & Beauducel, A. (2017). Worry-inducing stimuli in an aversive Go/NoGo task enhance reactive control in individuals with lower trait-anxiety. *Biological Psychology*, 125, 1-11.

- Leue, A., Lange, S., & Beauducel, A. (2012). Modulation of the conflict monitoring intensity: The role of aversive reinforcement, cognitive demand, and trait-BIS. *Cognitive, Affective, & Behavioral Neuroscience, 12*, 287-307.
- Leue, A., Weber, B., & Beauducel, A. (2014). How do working-memory-related demand, reasoning ability and aversive reinforcement modulate conflict monitoring? *Frontiers in Human Neuroscience, 8*, Article 210.
- Liepmann, D., Beauducel, A., Brocke, B., & Amthauer, R. (2007). *Intelligenz-Struktur-Test 2000 R* Göttingen: Hogrefe.
- Moser, J. S., Moran, T. P., Schroder, H. S., Donnellan, M. B., & Yeung, N. (2013). On the relationship between anxiety and error monitoring: A meta-analysis and conceptual framework. *Frontiers in Human Neuroscience, 7*, article 466.
- Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia, 9*, 97-113.
- Ridderinkhof, K. R., Ullsperger, M., Crone, E. A., & Nieuwenhuis, S. (2004). The role of the medial frontal cortex in cognitive control. *Science, 306*, 443-447.
- Shackman, A. J., Salomons, T. V., Slagter, H. A., Fox, A. S., Winter, J. J., & Davidson, R. J. (2011). The integration of negative affect, pain, and cognitive control in the cingulate cortex. *Nature Reviews, 12*, 154-165.
- Shenhav, A., Botvinick, M. M., & Cohen, J. D. (2013). The expected value of control: An integrative theory of anterior cingulate cortex function. *Neuron, 79*, 217-240.
- Shenhav, A., Cohen, J. D., & Botvinick, M. M. (2016). Dorsal anterior cingulate cortex and the value of control. *Nature Neuroscience, 19*, 1286-1291.
- Stanislaw, H., & Todorov, N. (1999). Calculation of signal detection theory measures. *Behaviour Research Methods, Instruments, & Computers, 31*, 137-149.
- Strobel, A., Beauducel, A., Debener, S., & Brocke, B. (2001). Psychometrische und strukturelle Merkmale einer deutschsprachigen Version des BIS/BAS Fragebogens von Carver und

- White [Psychometric and structural features of a German version of the BIS/BAS scales of Carver and White]. *Zeitschrift für Differentielle und Diagnostische Psychologie*, 22, 216-227.
- Süß, H.-M., Oberauer, K., Wittmann, W. W., Wilhelm, O., & Schulze, R. (2002). Working-memory capacity explains reasoning ability—and a little bit more. *Intelligence*, 30, 261-288.
- Vassena, E., Silvetti, M., VBoehlert, C. N., Achten, E., Fias, W., & Verguts, T. (2014). Overlapping neural systems represent cognitive effort and reward anticipation. *Plos one*, 9, e91008.
- Weldon, R. B., Mushlin, H., Kim, B., & Sohn, M.-H. (2013). The effect of working memory capacity on conflict monitoring. *Acta psychologica*, 142, 6-14.

Tables

Table 1. Pearson correlations (two-tailed) between trait-BIS and reasoning ability. The diagonal represents Cronbach's alpha.

	Trait-BIS	Reasoning ability
Trait-BIS	.83	
Reasoning ability	-.06 ns	.77

Note. All scales are normally distributed (Shapiro-Wilk: $p > .18$).

ns: not significant.

Table 2. Means and standard errors for behavioral data.

	M	SE
% correct responses		
Go stimuli	98.24%	0.44
Nogo stimuli	93.31%	0.95
Response times		
Low cognitive demand	199.79 ms	6.13
High cognitive demand	210.42 ms	5.67
Sensitivity d'		
Low cognitive demand	4.27	0.16
High cognitive demand	4.61	0.16
Number of errors (collapsed across Go and Nogo stimuli)		
Low error feedback	1.18	0.20
High error feedback	1.06	0.13

Note. Number of errors was analyzed with Mann-Whitney U test controlling for gender (similar to the between-subject factor inserted in the repeated measures ANCOVAs). All $ps \geq .39$.

Table 3. Summary of fMRI results with regard to a priori hypotheses, segregation hypothesis, and integrative hypothesis on ACC functioning.

A priori hypotheses (BOLD signal, beta weights)	Main effect / interaction	Result
H1: dACC: nogo > go	Region × Stimulus type	significant
H2: dACC: high cognitive demand > low cognitive demand	Region × Cognitive demand	ns
H3: rACC: more aversive error feedback > less aversive error feedback	Region × Error feedback	ns
H4: rACC: high cognitive demand > low cognitive demand in individuals with higher reasoning scores	Region × Cognitive demand × Reasoning	ns
H5: dACC: more aversive > less aversive error feedback in individuals with higher trait-BIS scores	Region × Error feedback × Trait-BIS	ns
Additional effects - segregation hypothesis (BOLD signal, beta weights)		
R1: dACC > rACC	Region	significant
R2: dACC _{go} > rACC _{go} for less aversive error feedback	ACC-region × Go-Nogo × Error feedback	significant
R3: dACC _{high demand} : nogo > go in individuals with higher reasoning scores	ACC-region × Stimulus type × Cognitive demand × Reasoning	significant
R4: rACC _{low demand} : individuals with higher Trait-BIS > lower Trait-BIS	ACC-region × Cognitive demand × Trait-BIS	significant

Additional effects - integrative hypothesis (BOLD signal, beta weights)

R1: dACC = rACC	Region	not confirmed
R2: High cognitive demand > low cognitive demand	Cognitive demand	ns
R3: More aversive error feedback > less aversive feedback	Feedback	ns
R4: High cognitive demand: higher Reasoning > lower Reasoning	Cognitive demand × Reasoning	ns
R5: More aversive error feedback: Higher Trait-BIS > lower Trait-BIS	Error feedback × Trait-BIS	ns

Note. dACC = dorsal ACC. rACC = rostral ACC. H = hypothesis. ns = non-significant. R = result. Significance level of main effects and interactions is reported for $p < .05$ and $p < .01$, respectively.

Figure captions

Figure 1. Summary of hypotheses. “+” = more intense conflict monitoring. “-“ = less intense conflict monitoring. H = hypothesis.

Figure 2. Trial sequences of the demand and feedback conditions of the go/nogo task.

Figure 3. Spherical and anatomical ROIs of the mid-sagittal section of all participants (dorsal ACC: purple, [0, 10, 46]) and rostral ACC (yellow, [0, 43, 12]).

Figure 4 A to D. Summary of main findings.

Figure 1.

Figure 2.

Figure 3.

Figure 4.

Supplement. Table S1.

Table S1. Repeated measures ANCOVA results for 15 mm and 10 mm spherical ROIs in accordance with Shackman et al. (2011) and Gray et al. (2005) without and with movement correction.

15 mm spherical ROIs with movement correction	10 mm spherical ROIs without movement correction	Mindboggle with movement correction (Klein & Tourville, 2012)	10 mm spherical ROIs with movement correction
A priori hypotheses			
H1: ACC-region $\times$ Stimulus type interaction:	H1: ACC-region $\times$ Stimulus type interaction:	H1: ACC-region $\times$ Stimulus type interaction:	H1: ACC-region $\times$ Stimulus type interaction:
$F(1,28) = 3.88, p = .06, \eta_p^2 = .12$	$F(1,28) = 5.92, p < .05, \eta_p^2 = .17$	$F(1,28) < 1, ns$	$F(1,28) = 5.15, p < .05, \eta_p^2 = .16$
Stimulus type main effect in dACC:	Stimulus type main effect in dACC:	No follow-up analyses	Stimulus type main effect in dACC:
$F(1,28) < 1, ns$	$F(1,28) < 1, ns$		$F(1,28) < 1, ns$
Stimulus type main effect in rACC:	Stimulus type main effect in rACC:		Stimulus type main effect in rACC:
$F(1,28) = 4.68, p < .05, \eta_p^2 = .14$	$F(1,28) = 8.69, p < .05, \eta_p^2 = .24$		$F(1,28) = 6.82, p < .05, \eta_p^2 = .20$
nogo- $M = 1.09, SE = 0.23$	nogo- $M = 1.09, SE = 0.23$		nogo- $M = 1.04, SE = 0.20$
go- $M = 0.83, SE = 0.18$	go- $M = 0.83, SE = 0.18$		go- $M = 0.81, SE = 0.17$

H2: ACC-region $\times$ Cognitive demand interaction:	H2: ACC-region $\times$ Cognitive demand interaction:	H2: ACC-region $\times$ Cognitive demand interaction:	H2: ACC-region $\times$ Cognitive demand interaction:
$F(1,28) < 1$, ns	$F(1,28) < 1$, ns	$F(1,28) < 1$, ns	$F(1,28) < 1$, ns
H3: ACC-region $\times$ Error feedback interaction:	H3: ACC-region $\times$ Error feedback interaction:	H3: ACC-region $\times$ Error feedback interaction:	H3: ACC-region $\times$ Error feedback interaction:
$F(1,28) < 1$, ns	$F(1,28) < 1$, ns	$F(1,28) < 1$, ns	$F(1,28) < 1$, ns
H4: ACC-region $\times$ Cognitive demand $\times$ Reasoning interaction:	H4: ACC-region $\times$ Cognitive demand $\times$ Reasoning interaction:	H4: ACC-region $\times$ Cognitive demand $\times$ Reasoning interaction:	H4: ACC-region $\times$ Cognitive demand $\times$ Reasoning interaction:
$F(1,28) < 1$, ns	$F(1,28) < 1$, ns	$F(1,28) = 1.15$, ns	$F(1,28) < 1$, ns
H5: ACC-region $\times$ Error feedback $\times$ Trait-BIS interaction:	H5: ACC-region $\times$ Error feedback $\times$ Trait-BIS interaction:	H5: ACC-region $\times$ Error feedback $\times$ Trait-BIS interaction:	H5: ACC-region $\times$ Error feedback $\times$ Trait-BIS interaction:
$F(1,28) < 1$, ns	$F(1,28) < 1$, ns	$F(1,28) < 1$, ns	$F(1,28) < 1$, ns

S1 continued.

15 mm spherical ROIs with movement correction	10 mm spherical ROIs without movement correction	Mindboggle with movement correction (Klein & Tourville, 2012)	10 mm spherical ROIs with movement correction
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Additional results

ACC-region (segregation hypothesis):	ACC-region (segregation hypothesis):	ACC-region (segregation hypothesis):	ACC-region (segregation hypothesis):
$F(1,28) = 13.01, p < .01, \eta_p^2 = .32$	$F(1,28) = 8.06, p < .01, \eta_p^2 = .22$	$F(1,28) = 76.38, p < .001, \eta_p^2 = .73$	$F(1,28) = 7.96, p < .01, \eta_p^2 = .22$
dACC: $M = 1.33, SE = 0.22$	dACC: $M = 1.69, SE = 0.29$	cACC: $M = 1.39, SE = 0.16$	dACC: $M = 1.61, SE = 0.27$
rACC: $M = 0.72, SE = 0.15$	rACC: $M = 0.96, SE = 0.20$	rACC: $M = 0.35, SE = 0.13$	rACC: $M = 0.93, SE = 0.18$
ACC-region $\times$ Stimulus type $\times$ Error feedback interaction:	ACC-region $\times$ Stimulus type $\times$ Error feedback interaction:	ACC-region $\times$ Stimulus type $\times$ Error feedback interaction:	ACC-region $\times$ Stimulus type $\times$ Error feedback interaction:
$F(1,28) = 11.32, p < .05, \eta_p^2 = .29$	$F(1,28) = 7.53, p < .05, \eta_p^2 = .21$	$F(1,28) = 2.93, p = .10, \eta_p^2 = .10$	$F(1,28) = 9.97, p < .01, \eta_p^2 = .26$
ACC-region $\times$ Stimulus type interaction	ACC-region $\times$ Stimulus type interaction	ACC-region $\times$ Stimulus type interaction	ACC-region $\times$ Stimulus type interaction
in conditions with less aversive error feedback:	in conditions with less aversive error feedback:	in conditions with less aversive error feedback:	in conditions with less aversive error feedback:
$F(1,28) = 15.55, p < .01, \eta_p^2 = .36$	$F(1,28) = 14.20, p < .01, \eta_p^2 = .34$	$F(1,28) = 2.90, p = .10, \eta_p^2 = .09$	$F(1,28) = 15.61, p < .001, \eta_p^2 = .36$

ACC-region main effect for Go stimuli, low error feedback:	ACC-region main effect for Go stimuli, low error feedback:	ACC-region main effect for Go stimuli, low error feedback:	ACC-region main effect for Go stimuli, low error feedback:
$F(1,28) = 24.00, p < .01, \eta_p^2 = .46$	$F(1,28) = 15.94, p < .01, \eta_p^2 = .36$	$F(1,28) = 62.23, p < .001, \eta_p^2 = .69$	$F(1,28) = 15.16, p < .01, \eta_p^2 = .35$
dACC: $M = 1.37, SE = 0.21$	dACC: $M = 1.73, SE = 0.28$	dACC: $M = 1.37, SE = 0.16$	dACC: $M = 1.68, SE = 0.26$
rACC: $M = 0.66, SE = 0.15$	rACC: $M = 0.82, SE = 0.18$	rACC: $M = 0.31, SE = 0.13$	rACC: $M = 0.82, SE = 0.18$
ACC-region main effect for Nogo stimuli, low error feedback:	ACC-region main effect for Nogo stimuli, low error feedback:	ACC-region main effect for Nogo stimuli, low error feedback:	ACC-region main effect for Nogo stimuli, low error feedback:
$F(1,28) = 6.66, p < .05, \eta_p^2 = .19$	$F(1,28) = 3.27, p = .08, \eta_p^2 = .11$	$F(1,28) = 60.89, p < .001, \eta_p^2 = .69$	$F(1,28) = 2.71, p = .11, \eta_p^2 = .09$
dACC: $M = 1.28, SE = 0.22$	dACC: $M = 1.60, SE = 0.28$	dACC: $M = 1.44, SE = 0.17$	
rACC: $M = 0.86, SE = 0.19$	rACC: $M = 1.16, SE = 0.25$	rACC: $M = 0.48, SE = 0.17$	
ACC-region $\times$ Stimulus type interaction in conditions with more aversive error feedback:	ACC-region $\times$ Stimulus type interaction in conditions with more aversive error feedback:	ACC-region $\times$ Stimulus type interaction in conditions with more aversive error feedback:	ACC-region $\times$ Stimulus type interaction in conditions with more aversive error feedback:
$F(1,28) < 1, ns$	$F(1,28) < 1, ns$	$F(1,28) < 1, ns$	$F(1,28) < 1, ns$

S1 continued.

15 mm spherical ROIs with movement correction	10 mm spherical ROIs without movement correction	Mindboggle with movement correction (Klein & Tourville, 2012)	10 mm spherical ROIs with movement correction
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Additional results

ACC-region × Stimulus type × Cognitive demand × Reasoning interaction:	ACC-region × Stimulus type × Cognitive demand × Reasoning interaction:	ACC-region × Stimulus type × Cognitive demand × Reasoning interaction:	ACC-region × Stimulus type × Cognitive demand × Reasoning interaction:
$F(1,28) = 2.55, p = .12, \eta_p^2 = .08$	$F(1,28) = 2.92, p = .10, \eta_p^2 = .09$	$F(1,28) = 2.23, p = .15, \eta_p^2 = .07$	$F(1,28) = 1.60, p = .22, \eta_p^2 = .05$
dACC:	dACC:	cACC:	dACC:
Stimulus type × Cognitive demand × Reasoning interaction:	Stimulus type × Cognitive demand × Reasoning interaction:	Stimulus type × Cognitive demand × Reasoning interaction:	Stimulus type × Cognitive demand × Reasoning interaction:
$F(1,28) = 9.91, p < .01, \eta_p^2 = .26$	$F(1,28) = 8.65, p < .01, \eta_p^2 = .24$	$F(1,28) = 6.15, p < .05, \eta_p^2 = .18$	$F(1,28) = 8.20, p < .01, \eta_p^2 = .23$

low demand, dACC:	low demand, dACC:	low demand, cACC:	low demand, dACC:
Stimulus type × Reasoning	Stimulus type × Reasoning	Stimulus type × Reasoning	Stimulus type × Reasoning
interaction:	interaction:	interaction:	interaction:
$F(1,28) = 2.63, p = .12, \eta_p^2 = .09$	$F(1,28) = 2.48, p = .13, \eta_p^2 = .08$	$F(1,28) = 2.71, p = .11, \eta_p^2 = .09$	$F(1,28) = 1.43, p = .24, \eta_p^2 = .05$
high demand, dACC:	high demand, dACC:	high demand, cACC:	high demand, dACC:
Stimulus type × Reasoning	Stimulus type × Reasoning	Stimulus type × Reasoning	Stimulus type × Reasoning
interaction:	interaction:	interaction:	interaction:
$F(1,28) = 5.95, p < .05, \eta_p^2 = .18 \Rightarrow$	$F(1,28) = 4.63, p < .05, \eta_p^2 = .14 \Rightarrow$	$F(1,28) = 1.44, p = .24, \eta_p^2 = .05 \Rightarrow$	$F(1,28) = 6.36, p < .05, \eta_p^2 = .19 \Rightarrow$
$r(38) = .33, p < .05$, more dACC activity	$r(38) = .28, p = .09$, more dACC activity	no follow up for cACC	$r(38) = .36, p < .05$, more dACC activity
in high demand conditions in individuals	in high demand conditions in individuals		in high demand conditions in individuals
with higher reasoning scores	with higher reasoning scores		with higher reasoning scores
rACC:	rACC:	rACC:	rACC:
Stimulus type × Cognitive demand ×	Stimulus type × Cognitive demand ×	Stimulus type × Cognitive demand ×	Stimulus type × Cognitive demand ×
Reasoning interaction:	Reasoning interaction:	Reasoning interaction:	Reasoning interaction:
$F(1,28) = 2.08, p = .16$	$F(1,28) = 1.84, p = .19$	$F(1,28) = 0.51, p = .48$	$F(1,28) = 2.20, p = .15$

ACC-region $\times$ Cognitive demand $\times$	ACC-region $\times$ Cognitive demand $\times$	ACC-region $\times$ Cognitive demand $\times$	ACC-region $\times$ Cognitive demand $\times$
Reasoning interaction:	Reasoning interaction:	Reasoning interaction:	Reasoning interaction:
$F(1,28) < 1$, ns	$F(1,28) < 1$, ns	$F(1,28) = 1.15$, ns	$F(1,28) < 1$, ns

S1 continued.

15 mm spherical ROIs with movement correction	10 mm spherical ROIs without movement correction	Mindboggle with movement correction (Klein & Tourville, 2012)	10 mm spherical ROIs with movement correction
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Additional results

ACC-region × Cognitive demand × Trait-BIS interaction:	ACC-region × Cognitive demand × Trait-BIS interaction:	ACC-region × Cognitive demand × Trait-BIS interaction:	ACC-region × Cognitive demand × Trait-BIS interaction:
$F(1,28) = 1.29, p = .27$	$F(1,28) = 7.74, p < .05, \eta_p^2 = .22$	$F(1,28) = 0.98, p = .33, \eta_p^2 = .03$	$F(1,28) = 1.76, p = .20, \eta_p^2 = .06$
rACC: Cognitive demand × Trait-BIS interaction:	rACC: Cognitive demand × Trait-BIS interaction:	rACC: Cognitive demand × Trait-BIS interaction:	rACC: Cognitive demand × Trait-BIS interaction:
$F(1,28) = 4.22, p < .05, \eta_p^2 = .13$	$F(1,28) = 4.58, p < .05, \eta_p^2 = .14$	$F(1,28) = 1.79, p = .19, \eta_p^2 = .06$	$F(1,28) = 3.91, p < .06, \eta_p^2 = .12$
dACC: Cognitive demand × Trait-BIS interaction:	dACC: Cognitive demand × Trait-BIS interaction:	cACC: Cognitive demand × Trait-BIS interaction:	dACC: Cognitive demand × Trait-BIS interaction:
$F(1,28) < 1, ns$	$F(1,28) < 1, ns$	$F(1,28) < 1, ns$	$F(1,28) < 1, ns$

<p>low demand, rACC more activated in individuals with higher trait-BIS scores:</p> <p>partial $r(34) = .36, p < .05$</p>	<p>low demand, rACC more activated in individuals with higher trait-BIS scores:</p> <p>partial $r(34) = .31, p = .06$</p>	<p>no follow up for rACC</p>	<p>low demand, rACC more activated in individuals with higher trait-BIS scores:</p> <p>partial $r(34) = .36, p < .05$</p>
<p>high demand, no differences between higher vs. lower trait-BIS in rACC:</p> <p>partial $r(34) = .12, ns$</p>	<p>high demand, no differences between higher vs. lower trait-BIS in rACC:</p> <p>partial $r(34) = .08, ns$</p>		<p>high demand, no differences between higher vs. lower trait-BIS in rACC:</p> <p>partial $r(34) = .12, ns$</p>
<p>Cognitive demand main effect, Error feedback main effect, Cognitive demand $\times$ Error feedback:</p> <p>$F_s < 1, ns$ (no evidence for integrative hypothesis)</p>	<p>Cognitive demand main effect, Error feedback main effect, Cognitive demand $\times$ Error feedback:</p> <p>$F_s < 1, ns$ (no evidence for integrative hypothesis)</p>	<p>Cognitive demand main effect, Error feedback main effect:</p> <p>$F_s < 1, ns$ (no evidence for integrative hypothesis)</p> <p>Cognitive demand $\times$ Error feedback:</p> <p>$F(1,28) = 2.14, p = .16$</p>	<p>Cognitive demand main effect, Error feedback main effect:</p> <p>$F_s < 1, ns$ (no evidence for integrative hypothesis)</p> <p>Cognitive demand $\times$ Error feedback:</p> <p>$F(1,28) = 2.51, p = .12$</p>

Note. dACC = dorsal anterior cingulate cortex. rACC = rostral anterior cingulate cortex. cACC = caudal anterior cingulate cortex.