Influences of Unconscious Priming on Voluntary actions: role of the Rostral Cingulate Zone

Martyn Teuchies[1], Jelle Demanet[1], Nura Sidarus[2], Patrick Haggard[2], Michaël A. Stevens[1], Marcel Brass[1].

[1] Department of Experimental Psychology, Ghent University, Belgium

[2] Institute of Cognitive Neuroscience, University College London, United Kingdom

Corresponding author at: Department of Experimental Psychology, Ghent University, Henri Dunantlaan 2, Belgium. Fax: +32 9 264 64 96.
E-mail address: martyn.teuchies@ugent.be (M. Teuchies).

Abstract

The ability to make voluntary, free choices is fundamental to what it means to be human. A key brain region that is involved in free choices is the rostral cingulate zone (RCZ), which is part of the medial frontal cortex. Previous research has shown that activity in this brain region can be modulated by bottom-up information while making free choices. The current study extends those findings, and shows, for the first time, that activation in the RCZ can also be modulated by subliminal information. We used a subliminal response priming paradigm to bias free and cued choices. We observed more activation in the RCZ when participants made a choice that went against the prime's suggestion, compared to when they chose according to the prime. This shows that the RCZ plays an important role in overcoming externally-triggered conflict between different response options, even when the stimuli triggering this conflict are not consciously perceived. Our results suggest that an important mechanism of endogenous action in the RCZ may therefore involve exerting an internally-generated action choice against conflicting influences, such as external sensory evidence. We further found that subliminal information also modulated activity in the anterior insula and the supramarginal gyrus.

1. Introduction

Making choices is a complex process. Every day we face an uncountable number of choices. Usually these are relatively unimportant: such as what to have for breakfast or what to wear to work. Nevertheless, every now and then we are faced with larger and more significant choices: such as where to live or what career to pursue. Being able to make such voluntary, or free, choices is fundamental for what it means to be human. Therefore, unsurprisingly, the question of how voluntary choices are established in the brain has fascinated researchers ever since the beginning of scientific psychology (James, 1892). In more recent years, much research has aimed to uncover the functional neuroanatomy of free choices, typically by comparing them with forced, or cued, choices (Forstmann, Brass, Koch, & von Cramon, 2006; Demanet, De Baene, Arrington, & Brass, 2013; Orr & Banich, 2014). A consistent finding is that the rostral cingulate zone (RCZ), part of the medial frontal cortex and extending posteriorly and dorsally from the anterior cingulate cortex (ACC), was consistently found to play a role in making voluntary choices. This region was interpreted as being important for choosing between different alternatives (Forstmann et al., 2006; Demanet et al., 2013; Brass and Haggard, 2008; Cunnington, Windischberger, Robinson, & Moser, 2006; De Baene, Albers, & Brass, 2012; Lau, Rogers, Ramnani, & Passingham, 2004; Mueller, Brass, Waszak, & Prinz, 2007; van Eimeren et al., 2006; Venkatraman, Rosati, Taren, & Huettel, 2009; Walton, Devlin, & Rushworth, 2004). Besides the RCZ, making voluntary choices has also been associated with activation in dorsolateral prefrontal cortex (DLPFC), anterior insula (AI), pre-supplementary motor area (pre-SMA), SMA-proper, inferior parietal lobule (IPL), and frontopolar cortex (FPC) (Forstmann et al., 2006; Demanet et al., 2013; Orr & Banich, 2014). These regions form a “choice network” that is part of a larger voluntary action network (Spence, Hunter, & Harpin, 2002; Brass & Haggard, 2008; 2010; Brass, Lynn, Demanet, & Rigoni, 2013; Krieghoff, Waszak, Prinz & Brass, 2011; Lau, Rogers, & Passingham, 2006). Another current research line focusses on whether or not voluntary choices are truly ‘free’ (Libet, Wright, & Gleason, 1982; Libet, Gleason, Wright & Pearl, 1983; Libet, 1985; 1999;

Soon, Brass, Heinze, & Haynes, 2008; Soon, He, Bode, & Haynes, 2013). Intuitively one would think that free choices are mostly determined by our own intentions and internal goals. Previous research, however, suggests that free choices may not be as free as they seem to be, and are strongly influenced by cues from the environment or past experiences (Bargh et al., 2001; Arrington & Logan, 2005; Arrington, Weaver & Pauker, 2010; Wenke, Fleming & Haggard, 2010; Orr & Weissman, 2011; Orr, Carp, & Weissman, 2012; Demanet et al., 2013; Orr & Banich, 2014). Wenke and colleagues (2010), for example, found that subliminal primes influence the responses on free choice trials in such a way that people responded significantly more slowly when they chose to act against the prime (in a prime-incompatible way). Participants were also significantly more likely to choose to follow the prime's suggestion (in a prime-compatible way), than go against the prime. Brain activity in the RCZ and the AI was reported to be reduced when a free choice is biased by supraliminal external information (Demanet et al., 2013; Orr & Banich, 2014). This research shows that some parts of the 'choice network' may be influenced by information that primes free choices. Previous studies, however, did not test whether a modulation of the choice network was also found when participants are completely unaware of the biasing information. In the present study we try to extend these findings by investigating how subliminally presented information might influence activation in the choice network with a particular focus on RCZ. The experimental paradigm was based on that of Vorberg et al. (2003). In the original paradigm, choices are always explicitly cued, in the sense that participants have to respond either with the right or the left hand to right or left pointing target arrows respectively. Before the target arrows, prime arrows are subliminally presented resulting in slower response times and more errors on incompatible trials, when the direction of the prime goes against the direction of the target (Vorberg et al., 2003). For the current study we adapted the paradigm following Wenke et al. (2010). In this adapted paradigm, participants additionally perform random trials on which they must freely choose between two response alternatives, without any cue indicating one over the other. In addition to the classic directional primes, we also included neutral primes, so as to distinguish costs of incompatible priming from benefits of compatible priming. Cued

choice trials and free choice trials were intermixed. The participant was asked to respond in a balanced and spontaneous way on free choice trials (Arrington & Logan, 2005; Demanet et al., 2013). Our main interest lay in contrasting cued choices with free choices. We predicted activation in the choice network, especially in the RCZ, for free choices over and above that for forced choices. We further investigated whether subliminal external information can have an effect on the involvement of these regions while making free and cued choices. First, we predicted that subliminal primes would affect the intentional choice network, with less activation when a prime-compatible choice is made (i.e. in the same direction as the prime) compared to prime-incompatible choice (i.e. against the direction of the prime). Furthermore, by using neutral primes we could test whether such a compatibility effect is driven by a facilitation effect in compatible trials or an interference effect in incompatible trials. Finally, we wanted to test whether such a modulation of the choice network is different for the free choice condition compared to the forced choice condition.

2. Method Section

2.1 Participants

Participants in this study were 30 Dutch-speaking students at Ghent University (20 female, mean age = 22.37 years, SD = 4.21); each reported as healthy and with no history of neurological, pain, or circulatory disorders and had normal or corrected-to-normal vision. All participants gave written informed consent, and the study was approved by the Medical Ethical Review Board of the Ghent University hospital, in accordance with the declaration of Helsinki. All participants were right-handed, as assessed by the Edinburgh Inventory (Oldfield, 1971), and were compensated thirty-five euros for their participation.

2.2 Stimuli

Stimulus presentation and response registration was done using Tscope software (Stevens, Lammertyn, Verbruggen, & Vandierendonck, 2006). In the scanner room the task was presented

using a Brainlogics 200MR digital projector that uses digital light processing (DLP) running at a refresh rate of 60 Hz with a viewing distance of 120 cm. Using DLP it only took 1 ms to deconstruct the image on the screen allowing our subliminal primes to be presented with greater accuracy. The duration of the primes was specified in ms. To make sure the primes were shown for only one refresh rate the duration of the primes was set to 10 ms. We logged the actual time the prime appeared on the screen for each trial. The mean presentation time was 17.94ms (*sd* = 0.28). The response priming task was adapted from Chambon (Chambon, Wenke, Fleming, Prinz, & Haggard, 2012). Three types of primes were used: grey coloured left or right pointing arrows or a neutral prime (which consisted of overlapping left and right pointing arrows). The primes were followed by superimposed by metacontrast masks of the same luminance (see Fig. 1). The metacontrast masks were embedded within target arrows that pointed left or right in cued-choice trials, or in both directions simultaneously in free-choice trials. Primes subtended visual angles of 0.8° x 1.86°, and the targets of 1.09° x 3.47° (Vorberg et al., 2003). Prime and target stimuli could appear randomly above or below a fixation cross at a visual angle of 1.38°. The unpredictable location was reported to enhance the masking effect (Vorberg et al., 2003).

2.3 Procedure

The priming procedure was similar to that used by Chambon et al. (2012) (figure 1). Participants were instructed to respond to the direction of the target arrows with their right and left index fingers using an MR compatible response box. On free-choice trials participants were encouraged to perform each action roughly equally often and not to use a fixed response strategy, such as alternating between responses. Examples of each target stimulus were presented before the experiment during instructions so that participants would be familiar with the targets before the experiment started for familiarization purposes. Participants were never alerted to the possibility of primes being presented, or influencing their behaviour. Primes were presented for 16.7 ms, followed by mask appearing with a stimulus onset asynchrony (SOA) of 33 ms. Target (and mask) duration was 250 ms. The response

window was set to 1500 ms. If participants failed to respond within this time window, they saw “te laat” (too late) for 1000 ms after the trial. The inter-trial-interval was jittered with values ranging between 1000ms and 5250ms. The distribution of the jitter values followed a distribution with pseudo-logarithmic density (range, 1000–5250 ms, in steps of 250 ms; mean jitter, 2625 ms). The task consisted of six blocks of 144 trials each. Cued- and free-choice trials were randomly intermixed within each block at a 50/50 ratio. In each block, half of the cued-choice trials were prime-response compatible and the other half were prime-response incompatible. For prime-response compatible trials, the direction of the prime was the same as the direction of the mask. In incompatible cued-choice trials, the response was again in the same direction of the mask, but in the opposite direction of the prime. In free-choice trials, compatibility was defined by the response of the participant, because on these trials there was no unambiguously ‘‘correct” response. Responses were labeled as prime-compatible when participants ‘‘freely” chose a response in the same direction as the prime, and incompatible when their response went against the direction of the prime. Thus, the meaning relation between prime and motor response was similar for compatible free-choice trials and for (correct) compatible forced choice trials (and ditto for incompatible trials). After the task participants were asked whether they noticed anything unusual about the stimuli during the task. None of the participants noticed the primes, but two participants reported seeing a “flash” before the target was presented. Following the test phase, participants were explicitly told about the presence primes, and performed a prime-visibility test. This test allowed us to check if the prime stimuli were indeed presented subliminally, or not. The prime-visibility test was similar to the one used by Wenke et al. (2010). In this test participants were asked to identify the direction of the primes (left or right) on each individual trial by using the same left and right response buttons as used during the test phase. This prime-visibility test was as similar as possible to the main response priming experiment. During this test, participants remained in the scanner, so environment and apparatus were identical to the main experiment. To minimize indirect priming effects on the recognition of the primes, participants were required to respond at least 600 ms after the mask was

presented. This also optimizes the conditions for recognition performance as speed stress could lead to reduced response accuracy (Vorberg et al., 2003). A visual cue ('*') signaled when they were allowed to respond. The test consisted of two blocks of 50 trials each. The responses to the primes were categorized using signal detection theory (Green & Swets, 1966). Measures of prime discriminability (d') for each participant were analysed.

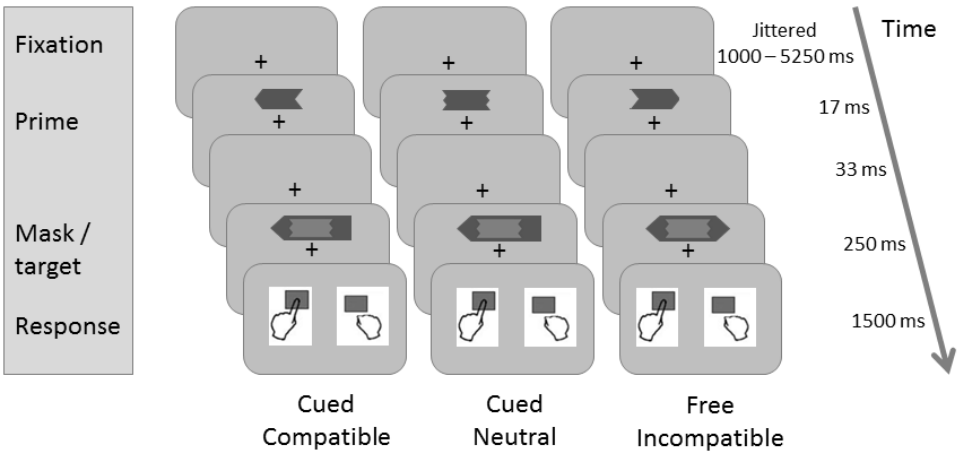

Figure 1. Schematic of trial procedure and stimuli, adapted from Wenke et al. (2010). Three example trials from the possible combinations of the factors choice type (cued: left and middle panel; free: right panel) and prime-action compatibility (compatible: left panel; neutral: middle panel; incompatible: right panel). In each example, the participant responded with the left hand. Participants were instructed to respond to the target stimuli, and were unaware of the presence of the arrow primes. Primes and targets could appear randomly above or below fixation on each trial.

2.4 fMRI data acquisition and preprocessing

Data were acquired with a 3T Siemens Magnetom Trio MRI system (Siemens Medical Systems, Erlangen, Germany) using a 32-channel radiofrequency head coil. Participants were positioned headfirst and supine in the magnet bore. First, 176 high-resolution anatomical images were acquired using a T1-weighted 3D MPRAGE sequence (TR = 2,250 ms, TE = 4.18 ms, TI = 900 ms, image matrix =

256 x 256, FOV = 256 mm, flip angle = 9°, and voxel size = 1 x 1 x 1 mm). Whole-brain functional images were then collected using a T2-weighted echo-planar imaging (EPI) sequence, sensitive to blood-oxygen-level dependent contrast (TR = 2,000 ms, TE = 35 ms, image matrix = 64 x 64, FOV = 224 mm, flip angle = 80°, slice thickness = 3.0 mm, distance factor = 17%, voxel size 3.5 x 3.5 x 3.0 mm, and 30 axial slices). A varying number of images were acquired per run due to individual differences in choice behavior and reaction times. All data were preprocessed and analyzed using Matlab and the SPM8 software (Wellcome Department of Cognitive Neurology, London, UK). To account for possible T1 relaxation effects, the first four scans of each EPI series were excluded from the analysis. The ArtRepair toolbox for SPM was used to detect outlier volumes concerning global intensity or large scan-to-scan movement (Mazaika, Whitfield-Gabrieli, & Reiss, 2007). First, a mean image for all scan volumes was created, to which individual volumes were spatially realigned using rigid body transformation. Thereafter, they were slice time corrected using the first slice as a reference. The structural image of each participant was coregistered with their mean functional image after which all functional images were normalized to the Montreal Neurological Institute (Montreal, Quebec, Canada) T1 template. Motion parameters were estimated for each session separately. The images were resampled into 3 x 3 x 3 mm voxels and spatially smoothed with a Gaussian kernel of 8 mm (full-width at half maximum). A high-pass filter of 128 Hz was applied during fMRI data analysis.

2.5 Behavioral Data Analysis

Mean reaction times (RTs) and error rates were submitted to a 2 X 3 repeated-measures ANOVA, with factors of choice type (cued vs. free) and prime-response compatibility (compatible vs. incompatible vs. neutral). We also analyzed response bias in free-choice trials. The response bias is expressed as the percentage of free-choice responses that were prime-compatible.

2.6 General GLM analyses

The participant-level statistical analyses were performed using the general linear model (GLM). Based on the 2x3 design of the response priming task (choice = cued/free x prime = compatible/incompatible/neutral), six different regressors of interest were modelled. For both the cued-choice and free-choice conditions compatible, incompatible and neutral trials were modelled separately. Erroneous trials and the first trials of each block were modeled as separate regressors of no interest (3.6% of the trials). For this analysis, the events of interest were the periods after the onsets of the different targets in the response priming task. Vectors containing the event onsets were convolved with the canonical hemodynamic response function (HRF) to form the main regressors in the design matrix (the regression model). Motion parameters for each individual subject were added. No derivatives were added to the HRF for this analysis. The statistical parameter estimates were computed separately for each voxel for all columns in the design matrix. Contrast images were constructed for each individual to compare the relevant parameter estimates for the regressors containing the canonical HRF. The group-level random effects analysis was then performed. Flexible factorial tests (Ashburner et al., 2010) were performed for each voxel of the contrast image. At the whole brain level, we only contrasted free-choice trials with cued-choice trials. This comparison was carried out to reveal the voluntary choice network, i.e. brain areas that were activated more during free-choice trials than during cued-choice trials. Only clusters significant at the familywise peak-level threshold of $p < .05$ are reported (initial voxel level threshold $T = 4.75$, $p < .001$). The resulting maps were overlaid onto a structural image of a standard MNI brain, and the coordinates reported correspond to the MNI coordinate system.

2.7 Regions of interest analyses

In the region of interest (ROI) analyses, we focused on the RCZ, as this was our principal ROI based on previous studies (Mueller et al., 2007; Lau et al., 2004; Krieghoff et al., 2009; Forstmann et al., 2006; Demanet et al., 2013). To create a ROI for the RCZ we averaged the coordinates that were reported

by the studies of Mueller et al. (2007), Lau et al. (2004) and Krieghoff et al. (2009) as these studies used a design that was similar enough to the design of the current study (Average MNI = [6 19 40], current study MNI = [6 20 43]). These studies all contrasted free choices with cued choices (In these studies, like in our current study, participants had to make a left or right response either freely or to external cues), as we did in our current study. Two of these studies reported coordinates in Talairach space, we converted these coordinates to MNI coordinates in MatLab using the tal2mni function (http://imaging.mrc-cbu.cam.ac.uk/imaging/MniTalairach; Duncan et al., 2000; Calder, Lawrence, & Young, 2001). Besides the RCZ we also looked at other brain regions that showed significant activation in whole brain analysis, and that are known to be part of the choice network. The actual ROIs were created using spheres with a 5mm radius around the peak voxels determined by the whole brain analysis (table 2). The percent beta change of each ROI was submitted to a 2 X 3 repeated-measures ANOVA, with factors choice type (cued vs. free) and prime-response compatibility (compatible vs. incompatible vs. neutral). When a significant main effect of prime-response compatibility (compatible vs. incompatible vs. neutral) was found, the differences between the conditions were analyzed post-hoc using two-tailed paired samples t-tests. Note that the interpretation of choice type is trivial because the ROIs were based on the main effect of choice type. Importantly, the compatibility factor is independent of the choice factor. Therefore the contrast used to define these ROIs is independent of the analysis of interest, thus avoiding concerns about "double-dipping" (Kriegeskorte, Simmons, Bellgowan, & Baker, 2009; Kriegeskorte, Lindquist, Nichols, Poldrack, & Vul, 2010) for the main effect of compatibility. The interpretation of the interaction of compatibility and choice, however, is more problematic, because this analysis is not independent of the main effect choice contrast used to define ROIs. This increased the risk of false positives, and would make problematic any interaction showing stronger effects of compatibility in the free than in the forced conditions.

3. Results

3.1 Behavioral Results

One participant was excluded because of an error rate of 20% in cued prime-compatible trials and 35% in the cued prime-incompatible trials. Three more participants were excluded from the analyses because their d' in the prime visibility test was larger than one standard deviation above the mean, indicating that unconscious perception could no longer be guaranteed. The remaining 26 (mean age 22.46 years, *SD* = 4.48; 19 female) participants that were unaware of the direction of the prime stimuli were included in the analysis. The d' values were not significantly different from zero (mean d' = 0.029 ± 0.21; one-sample t-test, t(26) = 0.70, $p = 0.49$). Participants failed to respond during the 1500 ms response window on 1.1% of the trials. For the remaining data, mean reaction times (RT) for correct trials were determined as a function of choice type (free, cued) and prime-response compatibility (compatible, incompatible or neutral). The reaction times were submitted to a 2 X 3 repeated-measures ANOVA with choice type (cued and free) and prime-response compatibility (prime-response compatible vs. incompatible vs. neutral) as factors. A Greenhouse-Geisser correction was used for tests involving the factor prime-response compatibility, which violated the ANOVA assumption of sphericity. This analysis yielded a significant main effect of choice type ($F(1, 25) = 27.06$, $p < .001$) and prime-response compatibility, ($F(2, 50) = 84.65$, $p < .001$). The significant main effect of choice type indicates that responses in the cued-choice condition were faster compared to the free-choice condition (free-cued= 17ms). The results (table 1) show a significant compatibility effect, such that prime-compatible responses were significantly faster ($t(25) = 10.27$, $p < .001$, $d = 0.41$) compared to prime-incompatible responses (incompatible – compatible= 27ms). Overall, directional primes led to a significant facilitation effect, such that prime-compatible responses were faster ($t(25) = 4.74$, $p < .001$, $d = 0.10$) than prime-neutral responses (neutral – compatible= 7ms); as well as a significant interference effect, with slower prime-incompatible responses ($t(25) = -9.17$, $p < .001$, $d = 0.32$) than prime-neutral responses (incompatible – neutral=

20ms). The interaction between choice type and prime-response compatibility was significant ($F(2, 50) = 14.58$, $p < .001$), indicating that for cued-choice trials the compatibility effect was smaller compared to free-choice trials (cued incompatible – cued compatible= 21ms, $t(25) = 9.24$, $p < .001$, $d = 0.33$; free incompatible – free compatible= 31ms, $t(25) = 9.07$, $p < .001$, $d = 0.45$). The same holds for the interference effect (cued incompatible – cued neutral= 11ms, $t(25) = 5.53$, $p < .001$, $d = 0.15$; free incompatible – free neutral= 27ms, $t(25) = 8.87$, $p < .001$, $d = 0.40$). Conversely, the facilitation effect was smaller in the free-choice trials, compared to cue-choice (cued compatible – cued neutral= 10ms, $t(25) = -5.57$, $p < .001$, $d = 0.18$; free compatible – free neutral= 4ms, $t(25) = -1.97$, $p = .060$, $d = 0.05$).

In the free-choice condition we also looked at how the primes biased the choices participants made. The response bias was defined as the percentage of trials in which participants' chose the prime-compatible as opposed to the prime-incompatible response. Participants chose the prime-compatible response option significantly more often (56.2%) than would be expected by chance, $t(25) = 5.51$, $p < .001$. The response bias also correlated positively ($r = .554$, $p < .01$) with the compatibility effect (on the reaction times) in the cued-choice condition (cued incompatible – cued compatible reaction times). This showed that more bias by the prime in free-choice trials (i.e. choosing more prime-compatible responses) was associated with greater interference by the prime, resulting in a larger compatibility effect, in cued-choice trials. The free-choice compatibility effect was not significantly correlated with the response bias, but it did show a significant positive correlation with the cued-choice compatibility effect ($r = .518$, $p < .01$). Looking at the error rates within the cued-choice condition, participants made significantly more errors ($t(25) = 4.57$, $p < 0.001$, $d = 0.77$) on prime-incompatible trials (7.84%) than on prime-compatible trials (3.82%).

To make sure participants did not use predetermined response strategies we looked at sequential dependencies between trials in the free-choice condition. We specifically looked at the free choice trials because the responses in the cued-choice condition are fixed, whereas in the free-choice condition participants have more opportunity to deviate from the instructions not to use

predetermined strategies. We compared the responses in the current free-choice trial (trial *n*) with those in the previous trial (trial *n*-1, which could either be a cued-choice trial or another free-choice trial) to see whether participants have a tendency to systematically respond either the same or the opposite in trial *n* as in trial *n*-1. We calculated the proportion of trials in which they made a switch to another response (from the left to the right hand or vice versa). Participants seem to have a tendency to switch to the other response rather than repeat the previous one (mean proportion of switches in free trials, $m = 0.57$). This finding is in line with previous research on the production of random response sequences (e.g. Nickerson, 2002). A frequently reported finding from studies that have looked into the concept of randomness is that participants, when asked to generate random binary sequences, have a tendency to produce sequences that consist of slightly more alternations than would be expected by chance (Nickerson, 2002). This is exactly what we observed in the current study, further supporting our conclusion that participants have been responding in a random way to the best of their abilities. The analysis also shows that participants are not more likely to switch when trial *n*-1 was a cued-choice trial ($m = 0.58$) compared to when it was a free-choice trial ($m = 0.57$, *paired samples* $t(25) = 0.67$, $p = .50$).

We also tested whether the instruction to respond as random as possible while using an equal amount of left and right responses might have interacted with the subliminal priming effect by introducing a constraint on the freedom of the choices. If the instruction to be random would interfere with the task then it is likely that participants would keep track of this random sequence during the task. This would imply that their choice would be more restricted towards the end of the block compared to the beginning and that the subliminal primes would become less effective. Hence, one would expect a reduction of the priming effect towards the end of a block. We carried out a linear mixed models analysis on the behavioral data to examine whether or not there was a reduction of the priming effect over the course of a block. In the analysis reaction time was the dependent variable and choice and compatibility were the predicting factors. Trial number was then added as a continuous predictor so we could look at the effect of compatibility over the course of a

block. We did not find a significant two-way interaction between trial number and compatibility ($F(2, 21297.3) = .203$, $p = .817$) nor did we find a significant three-way interaction between trial number, choice and compatibility ($F(2, 21304) = .075$, $p = .927$). This shows that the priming effect does not change over the course of a block thus suggesting that the instructions seem to have no or only a minimal impact on the choice process.

Table 1.

	Reaction time (ms)	% errors
Choice type: Cued Choice		
Compatible	426.8 (12.3)	3.82
Incompatible	448.3 (11.3)	7.84
Difference	21.5	4.02
	Reaction time (ms)	% Responses
Choice type: Free Choice		
Compatible	441.9 (14.1)	56.2
Incompatible	473.4 (13.4)	43.8
Difference	31.5	
Cued Neutral	436.5 (11.3)	
Free Neutral	446.2 (13.6)	
Difference	9.7	

Reaction times and percentage of errors as a function of choice type and prime-action compatibility.
Note: numbers in parentheses show standard errors of the means across participants

3.2 fMRI

3.2.1 Whole-Brain Analysis Results

In this analysis we focused on the brain regions that showed significant activity when contrasting free-choice related activity with cued-choice related activity. This way we wanted to identify which brain regions were involved in making free-choices. Several clusters were revealed that were activated more (family wise error (FWE) corrected) during free-choice trials compared to cued-choice trials (Table 2). In particular, we found a large cluster of activity of this kind in the rostral cingulate zone (RCZ). While the peak coordinates of this cluster (MNI 6 20 43) were in the right RCZ, this cluster also overlapped with peak coordinates reported in previous studies comparing free-choices and cued-choices (Mueller et al., 2007; Lau et al., 2004; Krieghoff et al., 2009; Forstmann et al., 2006; Demanet et al., 2013; Orr & Banich, 2014). We also found active clusters in the left anterior insula (AI; MNI -36 20 -2), left supramarginal gyrus (SG; MNI -48 -40 46), right SG (MNI 45 -37 40), right pre-supplementary motor area (pre-SMA; MNI 18 14 58), left pre-SMA (MNI -24 5 64), left dorsolateral prefrontal cortex (DLPFC; MNI -48 14 34) and the right DLPFC (MNI 51 14 28). Even though we were not primarily interested in looking at the interaction between choice and prime-compatibility at the whole brain level we did carried out the analysis for completeness but were unable to find any significant whole brain activation. Neither did we find significant whole brain activation when contrasting compatible versus incompatible choices.

Table 2.

Region	Peak Coordinates (MNI)	*z*-score	Extent
Free-choice > Cued-choice			
Right rostral cingulate zone	6 20 43	7.10	161
Left supramarginal gyrus	-48 -40 46	7.02	398
Right supramarginal gyrus	45 -37 40	6.79	339

Right pre-SMA	18 14 58	6.17	126
Left pre-SMA	-24 5 64	5.31	15
Left anterior insula	-36 20 -2	5.14	28
Left DLPFC	-48 14 34	5.13	34
Right DLPFC	51 14 28	4.95	12

Active regions on whole-brain level revealed by contrasting free-choice trials with cued-choice trials (cluster-level threshold $P < .05$, family-wise error correction, initial voxel level threshold $T = 4.75$, $p < .001$).

3.2.2 Region of Interest (ROI) Analysis Results

In order to investigate how subliminal primes influenced activity in the choice network, and particularly in the RCZ, we carried out two region of interest analyses, using an ROI that was based on previous studies that contrasted free choices with cued choices and one that was based on the whole brain contrast of free versus cued choice. In the independent ROI analysis a 2x3 repeated-measures ANOVA showed a significant main effect for prime-compatibility ($F(2, 24) = 4.07$, $p = .030$). There was no significant interaction between choice and prime-response compatibility. This region was more strongly activated in the incompatible prime-response condition compared to the compatible condition ($t(25) = -2.59$, $p = .016$, $d = .36$) and the neutral condition ($t(25) = 2.49$, $p = .020$, $d = .39$). The compatible and the neutral conditions did not differ in activation ($t(25) = -0.07$, $p = .95$, $d = .01$). In the second ROI analysis, we looked at the active clusters that were found in the contrast of free choices compared to cued choices during the whole-brain analysis. Here we were primarily interested in the influence of prime-response compatibility, given that the ROIs were selected on the basis of the main effect of choice type. A 2x3 repeated-measures ANOVA (choice x prime-compatibility) revealed a significant main effect of prime-response compatibility in the right RCZ ($F(2, 50) = 4.87$, $p = .012$). The RCZ showed an activation pattern consistent with a response-conflict interpretation (Fig. 2). This region was more strongly activated in the incompatible prime-response condition compared to the compatible condition ($t(25) = -3.01$, $p = .006$, $d = .56$) and the neutral

condition ($t(25) = 2.47$, $p = .020$, $d = .52$). The compatible and the neutral conditions did not differ in activation ($t(25) = -0.17$, $p = .87$, $d = .02$).

Looking at the whole-brain level analysis, several other regions were significantly more activated during free-choice trials, compared to cued-choice trials. These regions were the left AI, left and right pre-SMA, the left and right DLPFC and the left and right SG. Before looking at the patterns of activation in each ROI separately we carried out a 2x3x8 repeated-measures ANOVA (choice x prime-compatibility x ROI) thus including ROI as a factor. We observed significant main effects for ROI ($F(7, 19) = 4.08$, $p = .007$) and compatibility ($F(2, 24) = 4.51$, $p = .022$) as well as a significant interaction between ROI and compatibility ($F(14, 12) = 4.14$, $p = .009$). This allowed for planned comparisons within each ROI to look at the main effect of prime-compatibility. We performed separate 3x2 repeated-measures ANOVA's for each ROI. Here we observed a significant main effect of prime-response compatibility in the left AI ($F(2, 24) = 3.92$, $p = .026$), the left SG ($F(2, 39.9) = 4.40$, $p = .017$) and the right SG ($F(2, 50) = 4.36$, $p = .018$). We did not find a main effect for prime-response compatibility in the left ($F(2, 50) = 0.33$, $p = .72$) and right DLPFC ($F(2, 50) = 2.72$, $p = .09$) and in the left ($F(2, 50) = 1.14$, $p = .32$) and right pre-SMA ($F(2, 50) = 2.47$, $p = .11$) (Fig. 3). For the left SG a Greenhouse-Geisser correction was used for the factor prime-response compatibility, which violated the ANOVA assumption of sphericity. In the left AI and the left SG we observed a similar response conflict pattern as in the RCZ (Fig. 2). There was marginally more activation in the incompatible prime-response condition compared to the compatible condition (left AI: $t(25) = -2.00$, $p = .056$, $d = .20$; left SG: $t(25) = -2.06$, $p = .050$, $d = .18$), and significantly more than in the neutral condition (left AI: $t(25) = 2.59$, $p = .016$ $d = .25$; left SG: $t(25) = 2.77$, $p = .010$, $d = .16$). The compatible and the neutral conditions did not differ in activation (left AI: $t(25) = 0.50$, $p = .62$, $d = .05$; left SG: $t(25) = 0.16$, $p = .87$, $d = .01$). In the right SG the incompatible condition differed significantly from the neutral condition (right SG: $t(25) = 2.49$, $p = .020$, $d = .20$), and marginally from the compatible condition (right SG: $t(25) = -1.90$, $p = .069$, $d = .14$). As in the other ROI's, the compatible and the neutral conditions did not differ in activation (right SG: $t(25) = 1.30$, $p = .205$, $d = .01$). These results

indicate that, compared to neutral and compatible trials, the RCZ, the left AI and the left and right SG were engaged more during incompatible trials. This suggests that these regions are involved in detecting and/or resolving response conflict induced by the subliminal primes. The fact that we found no significant main effects of prime-response compatibility in the left and right pre-SMA and in the left and right DLPFC implies that at least in the current study the pre-SMA and the DLPFC were not directly involved in resolving conflict due to an external, subliminal bias.

Finally, out of the eight ROI's that were created, only one ROI (right SG) showed a marginally significant interaction between choice type and prime-response compatibility ($F(2, 24) = 3.13$, $p = .062$). Post-hoc paired-sample t-tests were carried out to investigate how the prime-response compatibility conditions differed from each other within the free-choice and the cued-choice conditions. We observed a significant difference between the free-choice compatible and incompatible prime-response conditions (See also figure 1; $t(25) = -2.10$, $p = .046$, $d = .18$) and between the free-choice incompatible and the neutral conditions ($t(25) = 2.56$, $p = .017$ $d = .23$), but not between the free-choice compatible and the neutral conditions ($t(25) = 0.46$, $p = .65$, $d = .04$). No significant differences were found between any of the prime-response compatibility conditions within the cued-choice condition, indicating that the interaction is driven by the differences between the free-choice prime-response incompatible condition with both the prime-response compatible and neutral condition. This finding is in line with the behavioral data, where we observed a similar interaction pattern (larger difference between prime-response incompatible and compatible free-choices compared to prime-response incompatible and compatible cued-choices). Of course, it should be noted that this interaction has to be interpreted with caution, if it can be interpreted at all. First of all it is only marginally significant. Secondly, interpretation is problematic because the selection of the ROIs is based on one factor of the interaction, namely choice type. Nevertheless, we thought it worthwhile to report it for completeness. Overall, our findings indicate that although we do find free-choice related brain activation in several areas that are related to voluntary action, for

both the cued-choice and free-choice conditions these areas appear to be similarly influenced by the primes. This indicates that similar processes could be involved in both choice conditions.

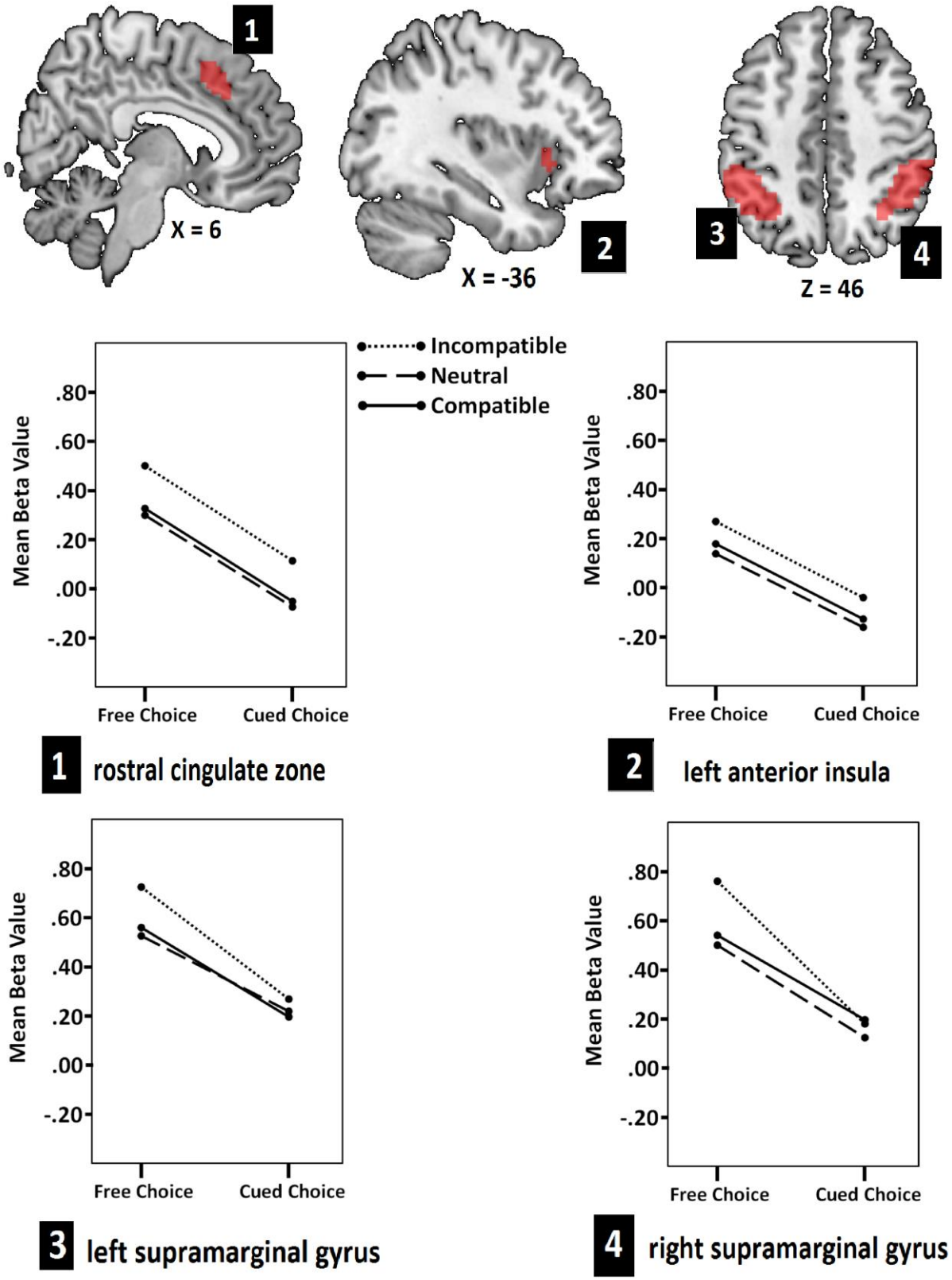

Figure 2. Areas that show a significant conflict activation pattern (incompatible significantly higher than compatible or neutral) on the whole brain level when contrasting free-choice related activation with cued-choice activation. The Y-axis depicts the beta values from the ROI. The peak-voxel coordinates used to define 5mm spherical ROI's are given in table 2.

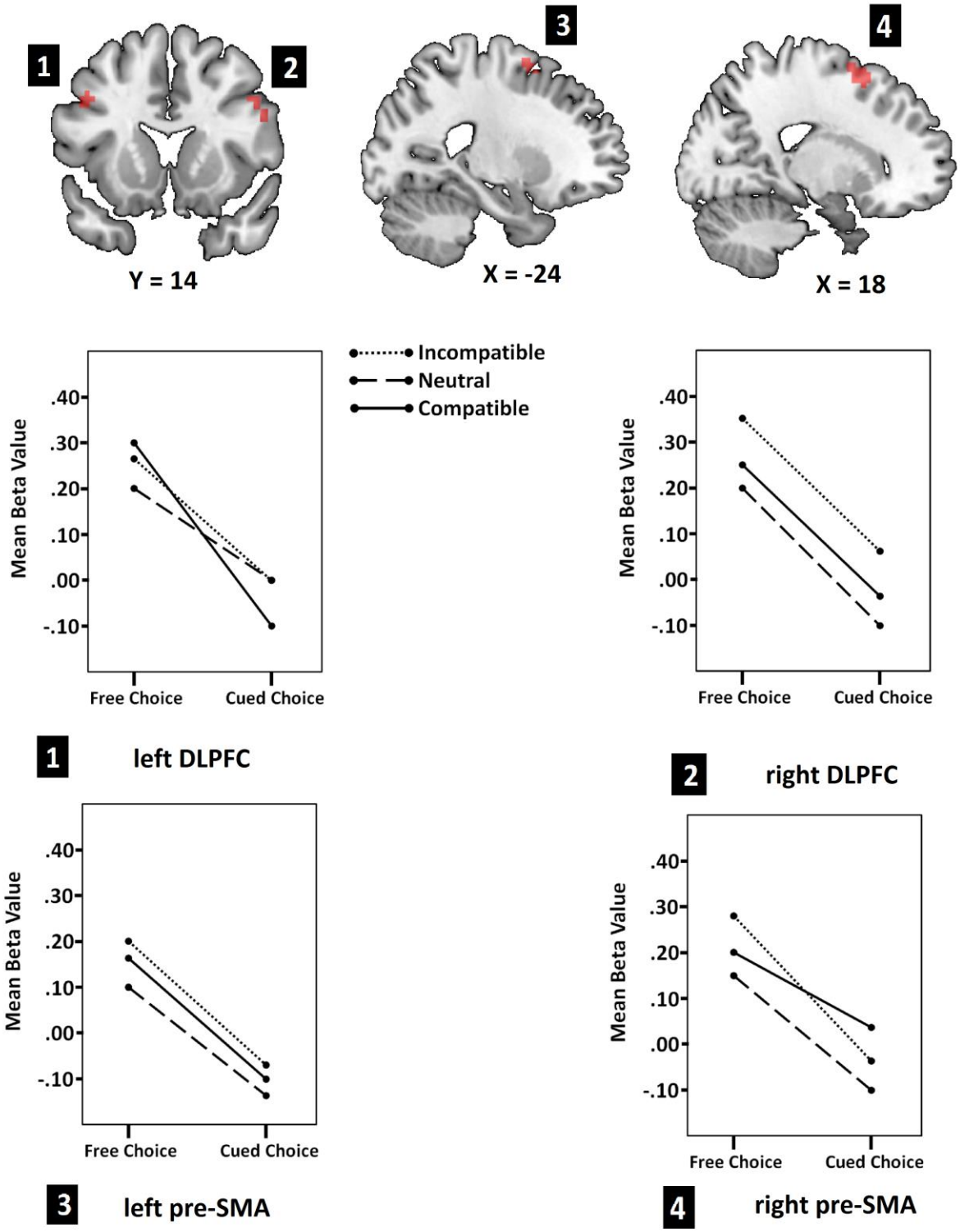

Figure 3. Areas that do not show a significant conflict activation pattern (incompatible significantly higher than compatible or neutral) on the whole brain level when contrasting free-choice related activation with cued-choice activation. The Y-axis depicts the beta values from the ROI. The peak-voxel coordinates used to define 5mm spherical ROIs are given in table 2.

4. Discussion

The primary aim of the current study was to investigate whether activation in the RCZ, a brain region that is part of a voluntary action network, can be influenced by subliminal information while carrying out an intentional action. We indeed found that activity in the RCZ, and a number of other brain regions associated with voluntary action, was modulated by subliminal primes. We used a free choice response priming paradigm (Wenke et al., 2010), in which participants made voluntary choices between equivalent alternative actions, while being exposed to subliminal primes. This paradigm consisted of intermixed cued-choice and free-choice trials. The behavioral results showed that in both cued-choice and free-choice conditions, the subliminal primes had an effect on the behavior of participants. Primes that opposed the direction of the response (incompatible prime-response condition) generally resulted in slower reaction times (and more errors on cued-choice trials) than primes that agreed with the direction of the response (compatible prime-response condition). These findings mirror the findings from previous response priming studies (see e.g. Vorberg et al., 2003; Wenke et al., 2010). The neutral prime condition lay between the incompatible and compatible conditions as regards RT. This suggests that the subliminal primes both interfered with the responses on incompatible trials and facilitated responses on the compatible trials. In the free-choice condition, participants also chose the prime-compatible response significantly more often than the prime-incompatible response (56% vs 44% respectively). Furthermore, we found that the primes elicited a stronger interference effect in free-choice trials compared to cued-choice, as indicated by the significant interaction between the factors choice type and prime-response compatibility on the reaction times. Previous studies using this paradigm (see Schlaghecken & Eimer, 2004; Wenke et al., 2010; O'Connor & Neill, 2011), however, did not find this interaction to be significant.

When contrasting free-choice related brain activity with cued-choice related brain activity on the whole brain level, we found activity in the RCZ, the left AI, the left and right DLPFC, the left and right pre-SMA and in the left and right SG (inferior parietal lobe, IPL). These brain areas have

previously been related to intentional choice (Demanet et al. 2013; Orr and Banich, 2014; Forstmann et al., 2006) and are thought to be part of an intentional action network (Seeley et al., 2007; De Pisapi et al., 2012). Hence we succeeded in our first goal of identifying involvement of the RCZ and other regions within the intentional choice network. Our experiment, however, primarily aimed to investigate whether subliminal primes can modulate activity in these brain regions. In ROI analyses, the RCZ showed a clear conflict activation pattern with more activation for choices that were prime-incompatible compared to prime-compatible or prime-neutral choices. In the left AI and the left SG we observed a significant difference between prime-incompatible and neutral choices and a marginally significant difference between prime-compatible and prime-incompatible choices. This might be interpreted as a somewhat weaker conflict pattern. These findings indicate that subliminal priming indeed modulates brain activity in regions that have previously been linked to voluntary action. Interestingly, this pattern was similar for free and cued choices, which suggests that incongruent subliminal primes not only induce stronger conflict in free-choice trials, but also in cued-choice trials. Of course it should be mentioned that this interpretation has to be treated with caution due to the fact that, except for the RCZ, the ROI's were created by contrasting free and cued choices. Our findings are in line with previous studies focusing on RCZ (De Pisapia et al., 2011) and AI (De Pisapia et al., 2011; Demanet et al., 2013; Orr & Banich, 2014) in resisting *external* influences. Interestingly, Demanet et al. (2013) did not find the RCZ to be more activated during incompatible trials compared to neutral and compatible trials. Rather they found a reduction of RCZ in activity during compatible trials compared to incompatible and neutral trials, indicating facilitation by the external information. This difference might be due to differences in the experimental paradigms. Demanet et al. (2013) used a voluntary task switching paradigm, in which participants had the opportunity to form associations between the external biasing information and the task. This means that, rather than introducing conflict, the external information could be facilitating decision making via these previously formed associations. Orr and Banich (2014), in contrast to Demanet et al. (2013), also found conflict activation patterns for incompatible trials. Although they also used a voluntary

task switching paradigm, they used flanker-style stimuli to introduce external biasing information. Similarly to the current study, flanker-style stimuli provide immediate online conflicting information, presumably causing the observed conflict activation patterns. We also found free-choice related activity in the DLPFC and the pre-SMA, but these regions did not show the conflict activation pattern we found in the RCZ, AI and the SG. The DLPFC and the pre-SMA are additional regions that have previously been associated with executive control (Cole & Schneider, 2007; Seeley et al., 2007; Demanet et al., 2013; Brass et al., 2013; Orr & Banich, 2014), but our findings suggest that they are not directly involved in overcoming conflict induced by unconscious primes. A study by Chambon et al. (2012) using subliminal response priming did not find the DLPFC to be involved in conflict resolution either. Instead, they observed more activation in the DLPFC in prime compatible trials compared to prime incompatible trials. While another study did find a conflict resolution pattern (Lau and Passingham, 2007), the DLPFC coordinates (MNI: -38, 36, 14) reported do not overlap with those reported in the current study (MNI: -48, 14, 34). This indicates that the present task activated a different part of the DLPFC, possibly reflecting different processes. Grey-matter density in the pre-SMA has previously been associated with compatibility effects on action for both supraliminal and strongly masked primes (Van Gaal et al., 2010). However, prime visibility was significantly above chance level, and a very different methodology was used compared to the present study. This again leaves open the possibility of different processes being at play in this region. Our results clearly suggest that subliminal information can modulate activity in brain regions associated with voluntary choice. We found activation in the RCZ and the AI to be associated with conflict induced by the subliminal primes. The RCZ has been associated with conflict monitoring before (Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004; Kerns, Cohen, MacDonald, Cho, Stenger, & Carter, 2004; Schouppe, Demanet, Boehler, Ridderinkhof, & Notebaert, 2014). However, our study extends these findings by showing that these regions are also sensitive to conflicts triggered by stimuli of which participants are completely unaware. It has been shown before that unconscious information can influence activity in regions associated with voluntary action (Lau & Passingham, 2007; Van Gaal,

Ridderinkhof, Fahrenfort, Scholte, & Lamme, 2008). In these previous studies, participants always performed externally guided, reactive behaviours, without any free-choice, voluntary component. The current study extends these findings to free choices. To our knowledge, ours is the first study to show that unconscious information has an impact on brain activity in regions that are involved in making free choices. Furthermore, we show that the RCZ and the AI are sensitive to intentional choice mode, and also to conflict induced by subliminal primes. Interestingly, we also found a marginally significant interaction between choice type and prime-response compatibility in the right SG, indicating that this region might be involved more during free choices than during cued choices, mirroring the response time pattern. The SG, which is part of the inferior parietal lobe (IPL), has been associated with making voluntary choices (Forstmann et al., 2006), and is thought to be part of a fronto-parietal action control network (Ruge, Brass, Koch, Rubin, Meiran, & von Cramon, 2005; Forstmann et al., 2006). As stated in the results section, however, this result should be interpreted with caution, because the interaction in this particular ROI is not independent of the definition of the ROI.

Taken together, our results suggest that conflict and choice might be two sides of the same coin. Choice necessarily implicates conflict, and conflict necessarily implicates choice. This might also explain why we did not find an interaction between choice and prime-compatibility in the RCZ. In both cued and free choices conflicting information was present so if the RCZ is mainly involved in conflict resolution it makes sense that it would also be involved in overcoming conflict in the cued choices. This involvement of the medial prefrontal cortex, of which the RCZ is a part, in both conflict and volition has been suggested before by Nachev, Rees, Parton, Kennard, & Husain (2005). According to Holroyd and Yeung (2012), the ACC associates outcome values with different response options, and chooses the appropriate option for the current environmental state. Via this process the ACC thus contributes to making a decision. It then directs the DLPFC to implement the chosen response option. Holroyd and Yeung (2012) also argue that the ACC determines the amount of effort invested in a response. Other studies have found more activity in the dACC during effortful behavior

(Mulert, Menzinger, Leicht, Pogarell, & Hegerl, 2005; Walton, Kennerley, Bannerman, Phillips, & Rushwortha, 2006). In the current study, we found activity in the RCZ (a region that extends posteriorly and dorsally from the ACC) by contrasting the free-choice condition with the cued-choice condition. Arguably, free-choice trials could be more effortful than forced choices, because they require an extra choice process. From this perspective, the RCZ would be responsible for the more effortful process of response selection and maintenance, while the DLPFC and the motor structures are responsible for implementing the choice (Holroyd & Yeung, 2012). In the current study we found that the DLPFC and the pre-SMA did not show heightened activity during prime-response incompatible choices compared to prime-compatible or prime-neutral choices. These areas might therefore be more involved in the execution and implementation of a chosen response than in the conflict resolution process. In contrast, our data suggest that RCZ and AI lie at the heart of a conflict resolution network, distinct from the response implementation network of DLPFC and pre-SMA. This dissociation is consistent with previous studies (Seeley et al., 2007; De Pisapia et al., 2011). In their terminology, RCZ and the AI are part of a salience network, while DLPFC and the pre-SMA are more involved in the execution of responses. Within this salience network, Seeley et al. (2007) also suggest a double role for the ACC and the AI. The first role is processing errors and conflicts. The second role is processing interoceptive feedback. On one view, the AI and RCZ monitor internal and external inputs and resolve conflict between competing options in order to choose the appropriate response.

Finally it is worth mentioning that the instructions to respond in a random, yet balanced way on free choice trials could have caused activation in the RCZ as well. This requirement could have introduced constraints on the supposedly free decision, and could have resulted in the engagement of the complex executive task of tracking recent responses and attempting to generate a random sequence. Activity in the RCZ has been associated with task difficulty (Wisniewski, Reverberi, Tusche, & Haynes, 2015). While we cannot completely rule out the possibility that participants used effortful strategies to produce random sequences, we think that it is unlikely that the RCZ activation we observed in the current study is driven by such strategies. First, the design mixes free choice trials

and cued trials. This reduces the likelihood that participants use complex strategies to determine a random order. Second, the important question for the current study is whether this requirement strongly constrains 'free' choices and whether this constraint interacts with priming? Looking at the behavioral data we found no evidence that the instruction to be random on free choices interfered with the task.

5. Conclusion

To conclude, our study has shown that the brain's voluntary action network can indeed be modulated by subliminal information. We thus propose that the RCZ and the AI are involved both in overcoming conflict between different response alternatives during free choices, here including those suggested by the external environment in the form of subliminal primes. We suggest that the DLPFC and the pre-SMA, in contrast, are responsible for implementing and carrying out the voluntary response chosen after such conflicts have been resolved.

6. Acknowledgements

The research reported in this paper was funded by the Interuniversity Attraction Poles Program initiated by the Belgian Science Policy Office (IUAPVII/33).

References:

Arrington, C. M., & Logan, G. D. (2005). Voluntary task switching: chasing the elusive homunculus. *Journal of Experimental Psychology Learning Memory and Cognition, 31,* 683–702.

Arrington, C. M., Weaver, S. M., & Pauker, R. L. (2010). Stimulus-based priming of task choice during voluntary task switching. *Journal of Experimental Psychology and Learning, 36*, 1060–1067.

Ashburner, J., Barnes, G., Chen, C.-C., Daunizeau, J., Flandin, G., Friston, K., et al. (2010). *SPM8 manual.* London: Functional Imaging Laboratory.

Brass, M., & Haggard, P. (2008). The what, when, whether model of intentional action. *Neuroscientist, 14,* 319–325.

Brass, M., & Haggard, P. (2010). The hidden side of intentional action: the role of the anterior insular cortex. *Brain Structure and Function, 214*, 603–610.

Brass, M., Lynn, M. T., Demanet, J., & Rigoni, D. (2013). Imaging volition: what the brain can tell us about the will. *Experimental brain research, 229,* 301–312.

Bargh, J. A., Gollwitzer, P. M., Lee-Chai, A., Barndollar, K., & Trotschel, R. (2001). The automated will: nonconscious activation and pursuit of behavioral goals. *Journal of Personality and Social Psychology, 81,* 1014–1027.

Bode, S., Murawski, C., Soon, C. S., Bode, P., Stahl, J., & Smith, P. L. (2014). Demystifying "free will": The role of contextual information and evidence accumulation for predictive brain activity. *Neuroscience and Biobehavioral Reviews, 47*, 636–645.

Calder, A. J., Lawrence, A. D., & Young, A. W. (2001). Neuropsychology of Fear and Loathing. *Nature Reviews Neuroscience*, *2*, 352–363.

Chambon, V., Wenke, D., Fleming, S. M., Prinz, W., & Haggard, P. (2012). An Online Neural Substrate for Sense of Agency. *Cerebral Cortex, 23,* 1031 – 1037.

Cole, M. W., & Schneider, W. (2007). The cognitive control network: integrated cortical regions with dissociable functions. *NeuroImage, 37,* 343–360.

Cunnington, R., Windischberger, C., Robinson, S., & Moser, E. (2006). The selection of intended actions and the observation of others' actions: a time-resolved fMRI study. *NeuroImage, 29,* 1294–1302.

De Baene, W., Albers, A. M., & Brass, M. (2012). The what and how components of cognitive control. *NeuroImage, 63,* 203–211.

Demanet, J., De Baene, W., Arrington, C. M., & Brass, M. (2013). Biasing free choices: the role of the rostral cingulate zone in intentional control. *Neuroimage, 72,* 207–213.

De Pisapia, N., Turatto, M., Lin, P., Jovicich, J., & Caramazza, A. (2011). Unconscious Priming Instructions Modulate Activity in Default and Executive Networks of the Human Brain. *Cerebral Cortex, 22,* 639–649.

Duncan, J., Seitz, R. J., Kolodny, J., Bor, D., Herzog, H., Ahmed, A., … Emslie, H. (2000). A neural basis for General Intelligence. *Science, 289*, 457–460.

Forstmann, B. U., Brass, M., Koch, I., & von Cramon, D. Y. (2006). Voluntary selection of task sets revealed by functional magnetic resonance imaging. *Journal of Cognitive Neuroscience, 18,* 388–398.

van Gaal, S., Scholte, H. S., Lamme, V. A. F., Fahrenfort, J. J., & Ridderinkhof, K. R. (2010). Pre-SMA Gray-matter Density Predicts Individual Differences in Action Selection in the Face of Conscious and Unconscious Response Conflict. *Journal of Cognitive Neuroscience, 23,* 382–390.

Green, D. M., & Swets, J. A. (1966). *Signal detection theory and psychophysics.* New York: Wiley.

Holroyd, C. B. & Yeung, N. (2012). Motivation of extended behaviors by anterior cingulate cortex. *Trends in Cognitive Sciences, 16,* 122–128.

James, W. (1892). *Psychology, a briefer course*. New York: Henry Holt and Company.

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.

Kriegeskorte, N., Simmons, W. K., Bellgowan, P. S. F., & Baker, C. I. (2009). Circular analysis in systems neuroscience: the dangers of double dipping. *Nature Neuroscience, 12,* 535–540.

Kriegeskorte, N., Lindquist, M. A., Nichols, T. E., Poldrack, R. A., & Vul, E. (2010). Everything you never wanted to know about circular analysis, but were afraid to ask. *Journal of Cerebral Blood Flow & Metabolism, 30,* 1551–1557.

Krieghoff, V., Waszak, F., Prinz, W., & Brass, M. (2011). Neural and behavioral correlates of intentional actions. *Neuropsychologia, 49*, 767–776.

Lau, H. C. & Passingham, R. E. (2007). Unconscious activation of the cognitive control system in the human prefrontal cortex. *Journal of Neuroscience, 27,* 5805–5811.

Lau, H. C., Rogers, R. D., & Passingham, R. E. (2006). Dissociating response selection and conflict in the medial frontal surface. *Neuroimage, 29,* 446–451.

Lau, H. C., Rogers, R. D., Ramnani, N., & Passingham, R. E. (2004). Willed action and attention to the selection of action. *NeuroImage, 21,* 1407–1415.

Libet, B. (1985). Unconscious cerebral initiative and the role of conscious will in voluntary action. *Behavior and Brain Sciences, 8,* 529–566.

Libet, B. (1999). Do we have free will? *Journal of Consciousness Studies, 6,* 47–57.

Libet, B., Gleason, C. A., Wright, E. W., & Pearl, D. K. (1983). Time of conscious intention to act in relation to onset of cerebral activity (readiness-potential). The unconscious initiation of a freely voluntary act. Brain, 106, 623–642.

Libet, B., Wright, E. W., & Gleason, C. A. (1982). Readiness potentials preceding unrestricted spontaneous pre-planned voluntary acts. *Electroencephalography & clinical neurophysiology, 54,* 322–5.

Mazaika P, Whitfield-Gabrieli, S., & Reiss A. (2007). Artifact repair for fMRI data from high motion clinical subjects. Poster presented at the 13th Annual Meeting of the Organization for Human Brain Mapping. Chicago, IL, June 10–14.

Mueller, V. A., Brass, M., Waszak, F., & Prinz, W. (2007). The role of the preSMA and the rostral cingulate zone in internally selected actions. *NeuroImage, 37,* 1354–1361.

Mulert, C., Menzinger, E., Leicht, G., Pogarell, O., & Hegerl, U. (2005). Evidence for a close relationship between conscious effort and anterior cingulate cortex activity. *The International Journal of Psychophysiology, 56,* 65–80.

Nachev, P., Rees, G., Parton, A., Kennard, C., & Husain, M. (2005). Volition and Conflict in Human Medial Frontal Cortex. *Current Biology, 15*, 122–128.

Nickerson, R. S. (2002). The Production and Perception of Randomness. *Psychological Review, 109,* 330–357.

O'Connor, P. A., & Neill, W. T. (2011). Does subliminal priming of free response choices depend on task set or automatic response activation? *Consciousness and Cognition, 20,* 280–287.

Oldfield, R. C. (1971). The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia, 9,* 97–113.

Orr, J. M., & Banich, M. T. (2014). The neural mechanisms underlying internally and externally guided task selection. *Neuroimage, 84,* 191–205.

Orr, J. M., Carp, J., & Weissman, D. H. (2012). The influence of response conflict on voluntary task switching: a novel test of the conflict monitoring model. *Psychological Research, 76,* 60–73.

Orr, J. M., & Weissman, D. H. (2011). Succumbing to bottom-up biases on task choice predicts increased switch costs in the voluntary task switching paradigm. *Frontiers in Psychology, 2,* 1–9.

Peyron, R., Laurent, B., & Garcia-Larrea, L. (2000). Functional imaging of brain responses to pain. A review and meta-analysis. Clinical Neurophysiology, 30, 263–288.

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.

Roskies, A. L. (2010). How does neuroscience affect our conception of volition? *Annual Review of Neuroscience, 33,* 109–130.

Ruge, H., Brass, M., Koch, I., Rubin, O., Meiran, N., & von Cramon, D. Y. (2005). Advance preparation and stimulus-induced interference in cued task switching: Further insights from BOLD fMRI. *Neuropsychologia, 43*, 340–355.

Schlaghecken, F., & Eimer, M. (2004). Masked prime stimuli can bias “free” choices between response alternatives. Psychonomic Bulletin & Review, 11, 463–468.

Schouppe, N., Demanet, J., Boehler, C. N., Ridderinkhof, K. N., & Notebaert, W. (2014). The Role of the Striatum in Effort-Based Decision-Making in the Absence of Reward. *The Journal of Neuroscience, 34,* 2148–2154.

Seeley, W. W., Menon, V., Schatzberg, A. F., Keller, J., Glover, G. H., Kenna, H., Reiss, A. L., & Greicius, M.D. (2007). Dissociable Intrinsic Connectivity Networks for Salience Processing and Executive Control. *The Journal of Neuroscience, 27,* 2349–2356.

Singer, T., Seymour, B., O'Doherty, J., Kaube, H., Dolan, R. J., & Frith, C. D. (2004). Empathy for pain involves the affective but not sensory components of pain. *Science, 303*, 1157–1162.

Soon, C. S., Brass, M., Heinze, H.-J., & Haynes, J.-D. (2008). Unconscious determinants of free decisions in the human brain. *Nature neuroscience, 11,* 543–545.

Soon, C. S., He, H. H., Bode, S., & Haynes, J.-D. (2013). Predicting free choices for abstract intentions. Proceedings of the national academy of sciences of the United States of America, 110, 6217–6222.

Spence, S. A., Hunter, M. D., & Harpin, G. (2002). Neuroscience and the will. Current Opinion in Psychiatry, 15, 519–526.

Stevens, M., Lammertyn, J., Verbruggen, F., & Vandierendonck, A. (2006). Tscope: a C library for programming cognitive experiments on the MS Windows platform. *Behavioral Research Methods, 38,* 280–286.

van Eimeren, T., Wolbers, T., Munchau, A., Buchel, C., Weiller, C., & Siebner, H. R. (2006). Implementation of visuospatial cues in response selection. *NeuroImage, 29,* 286–294.

Van Gaal, S., Ridderinkhof, K. R., Fahrenfort, J. J., Scholte, H. S., & Lamme, V. A. F. (2008). Frontal Cortex Mediates Unconsciously Triggered Inhibitory Control. *The Journal of Neuroscience, 6,* 8053–8062.

Venkatraman, V., Rosati, A. G., Taren, A. A., & Huettel, S. A. (2009). Resolving response, decision, and strategic control: evidence for a functional topography in dorsomedial prefrontal cortex. *Journal of Neuroscience, 29,* 13158–13164.

Vorberg, D., Mattler, U., Heinecke, A., Schmidt, T., & Schwarzbach, J. (2003). Different time courses for visual perception and action priming. *Proceedings of the national academy of sciences of the United States of America, 100,* 6275–6280.

Walton, M. E., Devlin, J. T., & Rushworth, M. F. (2004). Interactions between decision making and performance monitoring within prefrontal cortex. *Nature Neuroscience, 7*, 1259–1265.

Walton, M. E., Kennerley, S. W., Bannerman, D. M., Phillips, P. E. M., & Rushwortha, M. F. S. (2006). Weighing up the benefits of work: behavioral and neural analyses of effort-related decision making. *Neural Networks, 19,* 1302–1314.

Wenke, D., Fleming, S. M., & Haggard, P. (2010). Subliminal priming of actions influences sense of control over effects of action. *Cognition, 115*, 26–38.

Wisniewski, D., Reverberi, C., Tusche, A., & Haynes, J-D. (2015). The Neural Representation of Voluntary Task-Set Selection in Dynamic Environments. *Cerebral cortex, 25*, 4715–4726.