FACULTY OF PSYCHOLOGY
AND EDUCATIONAL SCIENCES

Interactions of conscious and unconscious processes in decision making

Martyn Teuchies

Supervisor: Prof. Dr. Marcel Brass
Co-supervisor: Prof. Dr. Jelle Demanet

Academic Year 2016-2017

A dissertation submitted to Ghent University in partial fulfilment of the requirements for the degree of Doctor of Psychology

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Guidance Committee

Prof. dr. Marcel Brass (Promoter)

Department of Experimental Psychology, Ghent University

Prof. dr. Jelle Demanet (Co-promoter)

Department of Experimental Psychology, Ghent University

Prof. dr. Ruth Krebs

Department of Experimental Psychology, Ghent University

Prof. dr. Jan De Houwer

Department of Experimental Clinical and Health Psychology, Ghent University

Prof. dr. Axel Cleeremans

Consciousness, Cognition, and Computation Group (CO3), Center for Research in Cognition and Neurosciences (CRCN), ULB Neuroscience Institute (UNI), Université libre de Bruxelles

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Ghent, September 1st 2017

Contents

General Introduction

The question of how we can voluntarily choose between different alternatives has fascinated researchers ever since the beginning of scientific psychology (James, 1892). Given the enormous amount of choices we face every day, this topic is highly relevant, yet relatively little is known about this fundamental human ability, especially about the interaction between typically unconscious bottom-up and often more conscious top-down factors both of which have been shown to influence how we make voluntary choices. But what exactly are voluntary, or free, choices? According to Bode et al. (2014) free choices intuitively seem to require independence from external constraints, or even from brain processes. For this reason many authors avoid the terms “free will” or “free choice”, but rather refer to “voluntary choices” or “internal decisions”. Haggard (2008) defines voluntary behavior by contrasting it with stimulus-driven behavior. Ideally voluntary behavior would be maximally stimulus-independent and lies at one end of a continuum with simple reflexes at the other end. Others have made this distinction between voluntary and stimulus-driven by referring to “active” free decisions and “passive” simple urges or desires (Batthyany, 2009). Unfortunately, a clear definition of what exactly free choices are is still lacking. Throughout this thesis I will refer to free choices as responses that are chosen by the participants themselves in the absence of (consciously perceived) external cues to guide them and that are opposed to cued choices where the response is clearly indicated by a target. Within psychology, two fields have been looking into how we make free choices, namely, cognitive neuroscience (see e.g. Brass & Haggard, 2008; Demanet, De Baene, Arrington, & Brass, 2013; Brass, Lynn, Demanet, & Rigoni, 2013; Orr & Banich, 2014) and social psychology (see e.g. Baumeister, Bratslavsky, Muraven, & Tice, 1998; Holland, Hendriks, & Aarts, 2005; Dijksterhuis, Bos, Nordgren, & van Baaren, 2006; Vohs & Schooler, 2008). Recent research in cognitive neuroscience suggests that free choices are influenced by both bottom-up and top-down factors (Demanet et al., 2013). Bottom-up factors refer to information (e.g. external cues) that influences free choices without the need to engage in explicit deliberation. Top-down factors refers to processes such as attention, intentions or a certain task-set that is activated during the experiment (Kiefer, 2007). It has been proposed that bottom-up and top-down factors can be dissociated at the brain level (Demanet et al., 2013). In their study, Demanet et al. (2013) found that when choices were influenced by bottom-up processes, the default mode network (DMN) (Raichle et al., 2001) was involved, and when choices were influenced by top-down processes the rostral cingulate zone (RCZ) was involved, which is part of the intentional action network (Brass & Haggard, 2008). Besides cognitive neuroscience, recent research in social psychology has also investigated how top-down and bottom-up factors influence free choices. For instance, even though we feel that our behavior seems to originate from conscious decisions, it has been demonstrated that voluntary decisions strongly depend on unconscious processes, such as external bottom-up influences (Custers & Aarts, 2010). This research has shown that goals themselves can arise and even operate unconsciously. Social situations or stimuli that are present in our surroundings can subliminally activate or prime certain goals in people’s minds. By priming social concepts, for instance, research has looked at how bottom-up information unconsciously influenced behavior (see e.g. Holland et al., 2005). Holland et al. (2005) found that participants who had been exposed to the smell of all-purpose cleaner were faster to indicate cleaning related words and showed more cleaning related behavior compared to a control group. Research in social psychology also looked at whether unconscious processing of information led to making better choices. In a study by Dijksterhuis et al. (2006) participants were prevented to think about complex problems by introducing a secondary task. It was found that choices were viewed as more favorable when they had been made in the absence of attentive deliberation. This showed that goals and the behavior to pursue them could be influenced by unconscious sources, and these goals did not have to be consciously set and adopted for them to start influencing our behavior (Custers & Aarts, 2010). A way in which social psychology has studied top-down influences on voluntary actions is by using a free-will-belief manipulation (see e.g. Baumeister et al., 2009; Rigoni, Kuhn, Sartori, & Brass, 2011). It has been shown that reading a text that questions the existence of free will (thereby reducing belief in free will) influenced intentional motor preparation, as reflected by a reduced readiness potential (Rigoni et al., 2011).

Response priming and bottom-up influences

To investigate how unconscious bottom-up influences affect our behavior previous studies have used a subliminal response priming paradigm (see e.g. Vorberg, Mattler, Heinecke, schmidt, & Schwarzbach, 2003; Sidarus, Chambon, & Haggard, 2013). This priming paradigm involves the presentation of subliminal primes that are masked by the target which doubles as a meta-contrast mask. Masked priming paradigms have already been around for several decennia to look at the impact of subliminal stimuli on behavior (Van den Bussche, Noortgate, & Reynvoet, 2009). Already in the early 1980's, Marcel (1983) observed that words were processed faster when they were preceded by other words that were semantically related (e.g. bike - car), but were presented subliminally by masking them and presenting them for a very short duration. In a typical response priming experiment (Figure 1) responses are 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 (see e.g. Vorberg et al., 2003; Sidarus et al., 2013). Before the target arrows, prime arrows are subliminally presented for a very short duration (16 ms) resulting in slower response times and more errors on

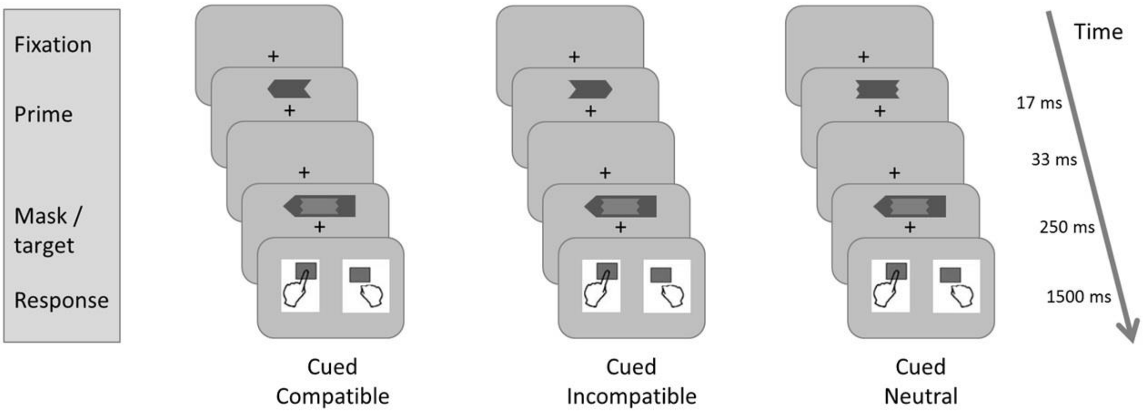

Figure 1. Schematic of the trial procedure and stimuli, adapted from Wenke et al. (2010). Three example cued-choice trials from the possible combinations of prime-response compatibility (compatible: left panel; incompatible: middle panel; neutral: right panel). In each example, the participant responded with the left hand.

incompatible trials, when the direction of the prime goes against the direction of the target, compared to compatible trials when the prime points in the same direction as the target (Vorberg et al., 2003; Schlaghecken & Eimer, 2004; Wenke et al., 2010; Sidarus et al., 2013; Furstenberg, Breska, Sompolinsky, & Deouell, 2015). Both the duration of the primes and the stimulus-onset asynchrony (SOA) between the prime and the mask are crucial for successful subliminal priming. Prime visibility increases with the duration of prime presentation and with the length of the SOA (Vorberg et al., 2003). The shorter the prime presentation and the SOA are, the better the chances the primes will remain subliminal. Previous studies have also looked at the effect that subliminal primes have on free choices (Schlaghecken & Eimer, 2004; Furstenberg et al., 2015; Wenke et al., 2010). In these studies the classical 'cued' response priming paradigm was adjusted (Figure 2) so that participants were asked to freely choose between two response alternatives with the only restriction to try and choose each alternative equally often. This was done by adding 'neutral' free-choice target arrows to the paradigm (not to be confused with neutral primes, which also can be added), which were arrows pointing both ways, indicating participants to freely choose a response. It has been shown that

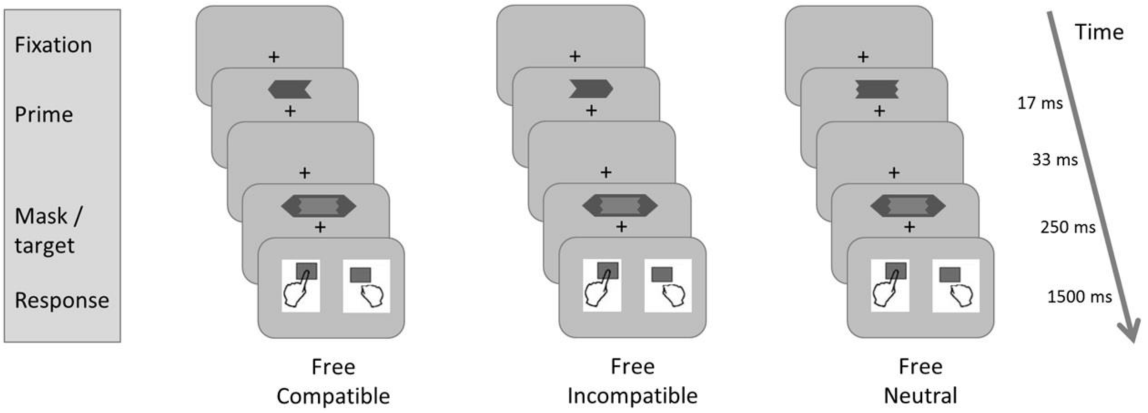

Figure 2. Schematic of the trial procedure and stimuli, adapted from Wenke et al. (2010). Three examples of free-choice trials from the possible combinations of prime-response compatibility (compatible: left panel; incompatible: middle panel; neutral: right panel). In each example, the participant responded with the left hand.

subliminal primes have the same impact on free choices as on cued choices; i.e. for both free choices and cued choices participants became slower and made more errors when the subliminal prime was incompatible with the response (Schlaghecken & Eimer, 2004; Furstenberg et al., 2015; Wenke et al., 2010). Also, in the free choice condition, participants typically showed a bias in their responses as they tended to choose the prime-compatible response significantly more often than the prime-incompatible response. Participants usually chose the prime-compatible response in 55% to 58% of the trials (Wenke et al, 2010; Furstenberg et al., 2015). Interestingly Schlaghecken and Eimer (2004) have shown that priming effects could only be found for free choices when you mixed them with cued choices. Blocks of only free choices showed no significant effects of the subliminal primes. This is consistent with a study by Wenke et al. (2010) who presented participants with blocks in which the ratio cued/free choices was either 25/75 or 75/25. They found larger priming effects (slower reaction times and more errors on incompatible trials compared to compatible trials) when the ratio cued/free choice trials was 75/25 compared to 25/75. To assess the visibility of the primes a prime-visibility test has often been used to obtain an objective measure of the participants' discriminative abilities (see e.g. Van den Bussche et al., 2009; Wenke et al., 2010). In this task participants had to categorize the subliminal primes instead of the targets by carrying out a response priming task in which they were instructed to respond in accordance with the direction of the primes, ignoring the target stimuli. Based on the categorization performance of the participants d' values could then be calculated, which served as a direct measure of prime visibility. This measure is based on signal detection theory (Green & Swets, 1966) and leads to a more conservative evaluation of prime visibility than a subjective method such as self-reports (e.g., Cheesman & Merikle, 1986). Mean d' values are typically computed per participant and they are positively correlated with prime visibility, such that invisibility of the primes corresponds with d' values that do not differ significantly from 0.

Free choices in the brain

It is clear that subliminal primes have an impact on our behavior, it is less clear still how subliminal response primes affect the brain and what regions are involved in processing this type of bottom-up information. Previous research has already tried to uncover the functional neuroanatomy of free choices, typically by comparing them with 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), has been found to play a role in making free choices (Figure 3).

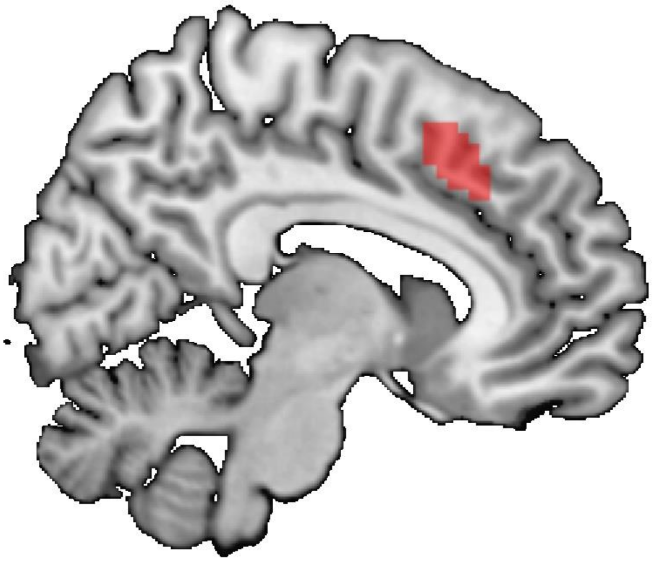

Figure 3. Location of the rostral cingulate zone (RCZ). X coordinate is 6.

Besides the RCZ, making free 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) and also overlaps with the multiple demand network, the essential function of which is to separate, organize, store and control the various parts of complex, intelligent mental activity (Duncan, 2010). Brass & Haggard (2008) introduced the What, When, Whether model (i.e. what response to choose? when to execute it? whether or not to execute it?) to explain intentional action. For this thesis the ‘What’ component is of most interest. The ‘what’ component of the model represents the decision about which action to execute. There is still some controversy about which brain region is involved in choosing the action, but when comparing brain activity in a free-choice condition with a cued-choice condition, the most consistent brain activity was found in the RCZ and pre-SMA (Lau, Rogers, Ramnani, & Passingham, 2004; Walton, Devlin, & Rushworth, 2004; Mueller, Brass, Waszak, Prinz, 2007). The RCZ has thus far been interpreted to be important for choosing between different response alternatives (Forstmann et al., 2006; Demanet et al., 2013; Brass & Haggard, 2008; Cunnington, Windischberger, Robinson, & Moser, 2006; De Baene, Albers, & Brass, 2012; Lau et al., 2004; Mueller et al., 2007; van Eimeren et al., 2006; Venkatraman, Rosati, Taren, & Huettel, 2009; Walton et al., 2004). However, RCZ activity has also been linked to conflict resolution rather than intentional processes (Botvinick, Braver, Barch, Carter, & Cohen, 2001; Nachev, Rees, Parton, Kennard, & Husain, 2005). This would indicate that the activation in the RCZ might reflect conflict between competing response options, rather than choosing which option to execute. Of course, competition between different response options would be a crucial aspect of the ‘what’ component (Botvinick et al., 2001; Nachev, Wydell, O’Neill, Husain, & Kennard, 2007), because in order to end up with a certain response, that response has to ‘win’ the conflict and be selected over alternative response options. In free choice situations such competition may be even stronger as there are no external cues to tell participants what to do, leading to a situation in which all options might have a similarly strong activation level (Brass & Haggard, 2008). Regarding the pre-SMA, Sumner et al. (2007) found that a patient with a specific SMA lesion was not able to inhibit unconscious competing responses. This would imply that the pre-SMA would be responsible for the automatic inhibition of competing response alternatives (Nachev et al., 2007; Brass & Haggard, 2008). Other studies have tried to dissociate response conflict from intentional action selection and have not yet found conclusive results. One study found that activity in the RCZ correlated more with conflict and that activity in the pre-SMA correlated more with action selection (Lau et al., 2006). Another study found this dissociation within the pre-SMA with activity in the more rostral part correlating with conflict and activity in a more caudal part correlating with action selection. This indicates that the roles of the RCZ and the pre-SMA are not yet clear in the context of voluntary action selection. What makes this dissociation especially difficult is that intentional action selection and response conflict may be so tightly linked together that it is impossible to look at one without the other. In other words, response conflict might be an inherent property of all action and intentional selection might necessarily be required in such situations (Brass & Haggard, 2008).

A number of studies have also been looking at brain activity preceding intentional choices (Libet, 1985; Soon, Brass, Heinze, & Haynes, 2008; Soon, He, Bode, & Haynes, 2013). These studies used relatively new neuroscientific methods such as multi-voxel pattern analysis (MVPA) to investigate to what extent preconscious processes determine free choices. The benefit of MVPA over conventional univariate fMRI analysis is that it is more sensitive since it does not require spatial averaging of individual voxels. Instead MVPA relies on pattern-classification techniques to extract patterns of brain activity across multiple voxels, even if the voxels might individually not be significantly active enough (Davis et al., 2014; Norman et al., 2006). Using MVPA one can discriminate between different events such as observing the direction of moving objects or even which of three categories the subject is thinking about during a memory retrieval task. This shows that MVPA can look at what is actually represented in a certain brain region rather than just showing that it becomes more or less activated in a specific experimental condition (Haynes and Rees 2006; Norman et al.

2006). Soon et al. (2008; 2013) used MVPA to investigate both which regions of the brain predetermine conscious intentions and at what time these intentions start to take shape. The tasks used by Soon et al. (2008; 2013) resembled that of Libet (see e.g. Libet, Wright, & Gleason, 1982; Libet, Gleason, Wright, & Pearl, 1983). Participants were asked to freely decide between one of two buttons (Soon et al., 2008) or between the execution of one of two tasks (Soon et al., 2013) when they felt the urge to do so. At the same time, they had to remember when they consciously made their motor decision by paying attention to a stream of letters. Using MVPA, Soon et al. (2008; 2013) found that they were able to predict free choices from activation patterns in the frontopolar cortex, precuneus, pre-SMA and SMA. The authors concluded that the medial frontopolar and precuneus/posterior cingulate regions were involved in the formation of high-level intentions for voluntary actions in general. This also shows that using MVPA to study voluntary actions seems to reveal the involvement of different regions then those found by studies using univariate analysis (see e.g. Wisniewsky, Goschke, & Haynes, 2016), which could be due to the methodological differences between MVPA and univariate fMRI analysis methods. Notwithstanding these methodological differences, Soon et al. (2008) showed that it was indeed possible to decode unconscious intentions from brain activity that precedes awareness of these choices, similar to the results of the classical Libet experiment (Libet, Wright, & Gleason, 1982; Libet, Gleason, Wright, & Pearl, 1983). According to Bode et al. (2014), however, the question remains as to whether a decision or action can ever be truly free, or whether it is always to some extent influenced by current and previous external constraints? Bode et al. (2014) further implied that the boundary between (unconscious) externally driven and conscious, or voluntary, self-generated actions is arbitrary, making it hard to be tested empirically. Therefore, an alternative interpretation of the results of the studies of Soon et al. (2008; 2013) suggested that it was not the preconscious intention that was decoded but rather an unconscious bias in the system that influenced free choices (Bode et al. 2014). The authors argued that even non-externally driven decisions and actions could be driven by internal needs and traits such as hunger, anxiety, personality traits, which were the inevitable result of interacting with the external world. Along the same lines it has been shown that there is a strong overlap between internal and external action control systems, as preparation for voluntary actions seems to facilitate stimulus-driven responses for instance (Hughes, Schutz-Bosbach, & Waszak, 2011). The question also arises as to how random and spontaneous people can respond in a free choice paradigm as it seems implausible that every single choice is independent of other choices that are made throughout the experiment (Bode et al., 2014). Some evidence indicates that neural activity preceding a trial is influenced for instance by memories of the previous trials or by preparatory processes for the next choice (Lages & Jaworska, 2012). It has also been shown that responding in a random manner is very difficult to accomplish (Lages & Treisman, 1998; Lages & Jaworska, 2012; Lages, Boyle, & Jaworska, 2013) and in light of an analysis of similar sequences of choices (Lages & Jaworska, 2012) the presence of unconscious response biases in the experiments of Soon et al. (2008; 2013) cannot be completely ruled out (Bode et al., 2014), leaving the question unanswered as to whether Soon et al. (2008; 2013) truly decoded voluntary intentions.

Combining bottom-up influences and top-down processing

Resolving conflict and intentional action selection intuitively implies some amount of conscious top-down intentional involvement, even if the conflict between response options is played out on a subliminal level. Nevertheless, subliminal priming has long been thought to be a fully automatic process that was unaffected by any conscious or top-down processes (Posner & Snyder, 1975; Schneider & Shiffrin, 1977). There are, however, indications that top-down processes such as attention, action intentions and the task-set that was active immediately before the presentation of the primes all have an influence on how subliminal bottom-up information is processed (Kouider & Dehaene, 2007; Kiefer, 2007). It has to be noted that, since the bottom-up information is unconsciously perceived, top-down modulation cannot intentionally take place in anticipation of the stimuli. Rather, top-down processes have an indirect influence for instance through previous reactions, current intentions, predictions, or instructions that activate a certain task-set (Kiefer, 2007). For instance, subliminal congruency effects in a numerical decision paradigm (Dehaene et al. 1998) disappeared if the prime did not appear at temporally predictable moments, thereby falling outside the temporal window of attention (Naccache, Blandin, & Dehaene, 2002). Similarly, in a series of word repetition priming experiments where the prime and the target could appear either at the same location or one below the other, priming effects were only found at attended locations (Lachter, Forster, & Ruthruff, 2004). It has also been found that using a pre-cueing procedure to manipulate attention to a subliminal prime increases priming effects (Sumner et al., 2006). These findings seem to offer ample evidence that allocation of attention is necessary for unconscious stimuli to trigger automatic processes and influence our behavior (Kiefer, 2007). Besides attention, priming effects are also modulated by intentions and task-sets that are active during the presentation of the masked prime (Kiefer, 2007). Task-set can be defined as an adaptive configuration of the cognitive system which is necessary to efficiently perform a given task (Rogers & Monsell, 1995; Gilbert & Shallice, 2002; Kiefer, 2007). According to Kiefer (2007) the concept of a “task set” is related to that of “intention”, but task-set is more specific as it refers to the immediate pursuing of a goal during task performance. The concept of “intention” is broader because it also includes the conscious representation of this goal as well as the commitment to perform a goal-related action (Ansorge & Neumann, 2005; Goschke, 2002; Kiefer, 2007). Subliminal primes are thought to only trigger responses when they match the currently active intentions of a person (Ansorge, Heumann, & Scharlau, 2002; Ansorge & Neumann, 2005). For instance, when task instructions where changed so that primes were no longer task-relevant, priming effects disappeared. If the target was black, then black-colored primes led to congruency effects. When the task-set then changed so that participants had to respond to red-colored targets, the black-colored primes did no longer influence reaction times to the target anymore. Based on their findings, Ansorge and Neumann (2005) thus argued that subliminal priming effects depend on the formation of action plans. Similarly, it was found that subliminal response priming effects in a semantic classification task were only observed for word categories that matched the current classification intention (e.g., living vs. non-living), but not for categories that were irrelevant such as pleasant vs. unpleasant (Eckstein & Perrig (2007). Closely related to task-set activation is the design of the response priming task itself, which can also have an influence on the priming effects via top-down processes. For instance, Jaśkowski, Skalska, and Verleger (2003) found that the size of subliminal response priming effects depended on the proportion of incompatible trials in the task. A high proportion of incompatible trials, which increased the probability of committing an error, resulted in reduced subliminal response priming effects in comparison to a low proportion of incompatible trials. Jaśkowski et al. (2003) argued that unconscious response priming processes were under strategic control and ERP effects suggested that top-down control modulated sensory processing of the masked primes thereby suggesting that a top-down gating mechanism was evoked when unconscious priming led to unwanted response tendencies. This mechanism then suppressed sensory prime processing as well as further automatic response preparations.

Metacognition and its neural correlates

So far, based on previous studies, it seems clear that top-down processes can modulate the influence of subliminal bottom-up information. Of course, the question arises to what extent participants can exert direct control over conflict caused by subliminal primes when the primes causing this conflict are largely inaccessible to participants' awareness. Can participants sense conflict without being aware of the causes of this conflict? Recent research has addressed this question by investigating a process called metacognition (Desender, Van Opstal, & Van den Bussche, 2014; Desender, Van Opstal, Hughes, & Van den Bussche, 2016). Generally speaking metacognition refers to the subjective experiences of our actions and has often been studied in relation to memory formation (see e.g. Metcalfe & Finn, 2008), memory retrieval (see e.g. Díaz, Lindín, Galdo-Alvarez, Facal, & Juncos-Rabadán, 2007), the sense of confidence during decision making (de Gardelle & Mamassian, 2014;

Fleming & Lau, 2014; Fleming, Weil, Nagy, Dolan, & Rees, 2010) or awareness of errors during decision making (Boldt & Yeung, 2015; Steinhauser & Yeung, 2010). One particular type of metacognition is the experience of fluency in action-selection. This type of metacognition has been studied before by using a subliminal response priming paradigm to manipulate fluency of action-selection by creating a subliminal conflict between two response options. To obtain a meta-cognitive judgement about the difficulty of the response, participants were asked on a trial-by-trial basis how hard it was for them to respond as fast and as accurately as possible to the target arrows (Desender et al., 2014; 2016). Participants rated incompatible trials (trials where the prime interfered with the response selection) as more difficult than compatible trials, showing that people could somehow become conscious of the conflict, or at least of the fact that it made responding correctly harder, even if they were unaware of the presence of the primes. On the neural level it is less clear what happens as the neural correlates of the metacognitive awareness of response conflict have not yet been unequivocally revealed. A study by Desender et al. (2016) found that the subjective sense of difficulty during action-selection correlated with an ERP component called the N2 which has been linked to ACC activity (Van Veen & Carter, 2002; Ullsperger, Fischer, Nigbur, & Endrass, 2014; Jiang, Zhang, & van Gaal, 2015). The ACC in turn has been linked to response competition and conflict monitoring (Kiehl et al., 2000; van Veen, Cohen, Botvinick, Stenger, & Carter, 2001; Botvinick, Braver, Barch, Carter, & Cohen, 2001; Barch, Braver, Sabb, & Noll, 2000; Cohen, Botvinick, & Carter, 2000; MacDonald, Cohen, Stenger, & Carter, 2000; Botvinick, Nystrom, Fissell, Carter, & Cohen, 1999; Carter, Braver, Barch, Botvinick, Noll, & Cohen, 1998; Carter, MacDonald, Botvinick, Ross, Stenger, Noll, & Cohen, 2000; Van Veen & Carter, 2002). The question that automatically arises is whether metacognition and conflict can be dissociated from each other? One possible solution of course would be to investigate whether conflict detection and metacognitive judgments of conflict are based on overlapping neural substrates. There may be some evidence for a neural dissociation between conflict detection and metacognition. As stated before, imaging research on conflict monitoring has found ample evidence that the ACC is strongly involved in monitoring behavior.

Imaging research on metacognition on the other hand seems to have found some evidence that the anterior prefrontal areas are involved in metacognition (Fleming & Dolan, 2012), or that the neural substrates of metacognition are domain-specific (McCurdy et al., 2013). However, the neural correlates concerning metacognitive awareness of response conflict have yet to be revealed. Thus, it remains an open question whether conflict detection and metacognitive experience of conflict have dissociable neural correlates.

Chapter overview and research objectives

Despite efforts from cognitive neuroscience and social psychology a clear understanding of the processes involved in making free choices is still lacking, especially regarding bottom-up and top-down processes and how they interact. Based on previous studies a subliminal response priming paradigm seemed the most suitable paradigm to look at the impact of unconscious bottom-up factors on free choices. This paradigm seems to yield robust priming effects and can be easily combined with top-down manipulations to study their modulating effect in the context of free choices. It has also been shown that certain brain regions such as the RCZ play an important role in free choices, but its exact functional role in voluntary action remains a matter of debate. Using subliminal response priming combined with top-down manipulations and data collection methods such as fMRI, the present thesis aims to answer some of these open issues. In the first two studies we focused on the bottom-up factors that influence free choices. Next, in chapter 3 we looked at top-down processes and specifically at how disrupting these top-down processes affected bottom-up influences on free choices. Finally, we wanted to look into the neural correlates of metacognitive awareness of response conflict.

Chapter 1

The first empirical chapter looks into how unconscious bottom-up factors influence free choices and which brain regions are involved. Previous studies have shown that the RCZ seems to play a crucial role in making free choices, but its exact function remains a matter of debate. This first experiment aims to further clarify the role of the RCZ in making free choices by collecting fMRI data from participants performing the response priming task. The priming paradigm used in this experiment is an adaptation from the paradigm used by Wenke et al. (2010). On top of the classical cued targets that point either left or right they added neutral 'free choice' targets that point both ways, indicating that participants could freely decide which response (left or right) they wanted to use. Additionally we also added neutral primes (primes without directional information) that could serve as a baseline measure. By comparing the reaction times of compatible and incompatible trials to the reaction times of the neutral trials we could calculate facilitation effects (difference between compatible trials and neutral trials) and interference effects (difference between incompatible trials and neutral trials). Furthermore, we investigated how brain areas that have been associated with making intentional choices are affected by such subliminal primes.

Chapter 2

A number of studies have been looking at brain activity preceding intentional choices (Soon et al., 2008; 2013). These studies used MVPA to investigate to what extent preconscious processes determined free choices. Predictive information was found in the precuneus, frontopolar cortex, pre-SMA and SMA, showing that it was indeed possible to decode pre-conscious intentions from brain activity that precedes awareness of these choices (Soon et al. 2008). However, an alternative interpretation of the results suggests that it is not an unconscious intention that is decoded but rather an unconscious bias in the system that influenced the free choices (Bode et al. 2014). The main aim of this chapter was to investigate how unconscious biases affect decoding of response alternatives from brain activity. In order to do so, we reanalyzed the data from chapter 1 using MVPA to investigate how an unconscious bias influenced the decoding of response alternatives both in free-choice and in cued-choice trials. We wanted to investigate whether unconscious biases influenced the decoding accuracy from patterns of brain activity in areas that were identified by Soon and colleagues (2008). Furthermore, we wanted to investigate whether areas that have been related to intentional choice in univariate analyses, were involved in encoding response alternatives.

Chapter 3

Another question that remains largely unanswered is to what extent bottom-up factors such as subliminal primes are modulated by top-down factors while making free choices. Previous research looking into top-down influences on subliminal priming has not yet looked at voluntary behavior, but only at tasks that have clear instructions and cues that guide participants' responses. It has been shown that a choice that was influenced by top-down processes required a certain amount of intentional involvement, such as allocating attention to the prime location, or keeping a task-set activated. The question is what would happen when, in the context of a free choice, only the intentions of the participants were manipulated, but task-set activation and attention to the primes were left the same? We expected that in this situation the subliminal priming effects would increase as there would be more room for the subliminal bottom-up influences such as primes to have an effect. To look into this, we combined the subliminal response priming paradigm with an anti-free-will belief manipulation (see e.g. Vohs & Schooler, 2008; Rigoni et al., 2011), which is a manipulation that originates from the field of social psychology. In this manipulation, half of the participants were asked to read a scientific text questioning free will, stating that free will is an illusion. The other half, functioning as a control group, read a scientific text that did not mention free will at all. Participants then performed the free choice subliminal response priming paradigm so we could investigate the impact of this top-down manipulation on the processing of the subliminal bottom-up information. The idea here was that this manipulation would reduce belief in free-will, thereby acting on the intentions of the participants. A reduced belief in free-will would thus lead to less intentional involvement, which in turn could lead to an increased bottom-up influence on behavior because participants could be more susceptible to the subliminal primes if they were less willing to choose a response themselves. Crucially, attentional allocation to the primes and task-set activation were not expected to change, so sufficient conditions for the primes to have an effect were still present.

Chapter 4

In the final chapter we wanted to look at the subjective experience of subliminal response conflict and more specifically the neural correlates of this experience as they have not yet been investigated. It also remains an open question whether conflict detection and metacognitive experience of conflict have dissociable neural correlates. In this experiment we looked at fluency of action-selection which we manipulated using subliminal response priming. We asked participants on a trial-by-trial basis how hard it was for them to respond as fast and as accurate as possible to the target stimuli, thereby obtaining metacognitive measures about the subjective difficulty of the responses. In this experiment we only used cued-choices, as during pilot experiments we found no reliable differences in subjective difficulty ratings between the free choice conditions. We then correlated these subjective difficulty ratings with neural activity to see which brain regions showed increased activity with increased subjective difficulty and whether these were the same brain regions that were also found to be active for subliminal response conflict such as the RCZ.

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Influences of Unconscious Priming on Voluntary actions: role of the Rostral Cingulate Zone[1]

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.

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[1] Teuchies, M., Demanet, J., Sidarus, N., Haggard, P., Stevens, M. A., & Brass, M. (2016). Influences of Unconscious Priming on Voluntary actions: role of the Rostral Cingulate zone. *Neuroimage*, *135*, 243–252.

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.

Method Section

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.

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).

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.

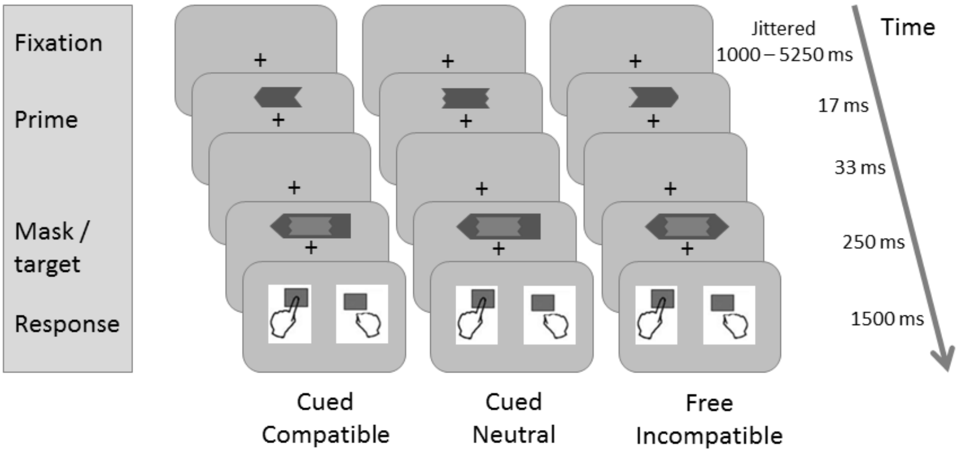

Figure 1. Schematic of trial procedure and stimuli, adapted from Wenke et al. (2010). Three example trials from the possible combinations of the factors choice type (cued: left and middle panel; free: right panel) and prime-action compatibility (compatible: left panel; neutral: middle panel; incompatible: 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.

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.

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.

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.

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.

Results

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

fMRI Results

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 $T = 4.75$, $p < .001$).

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.

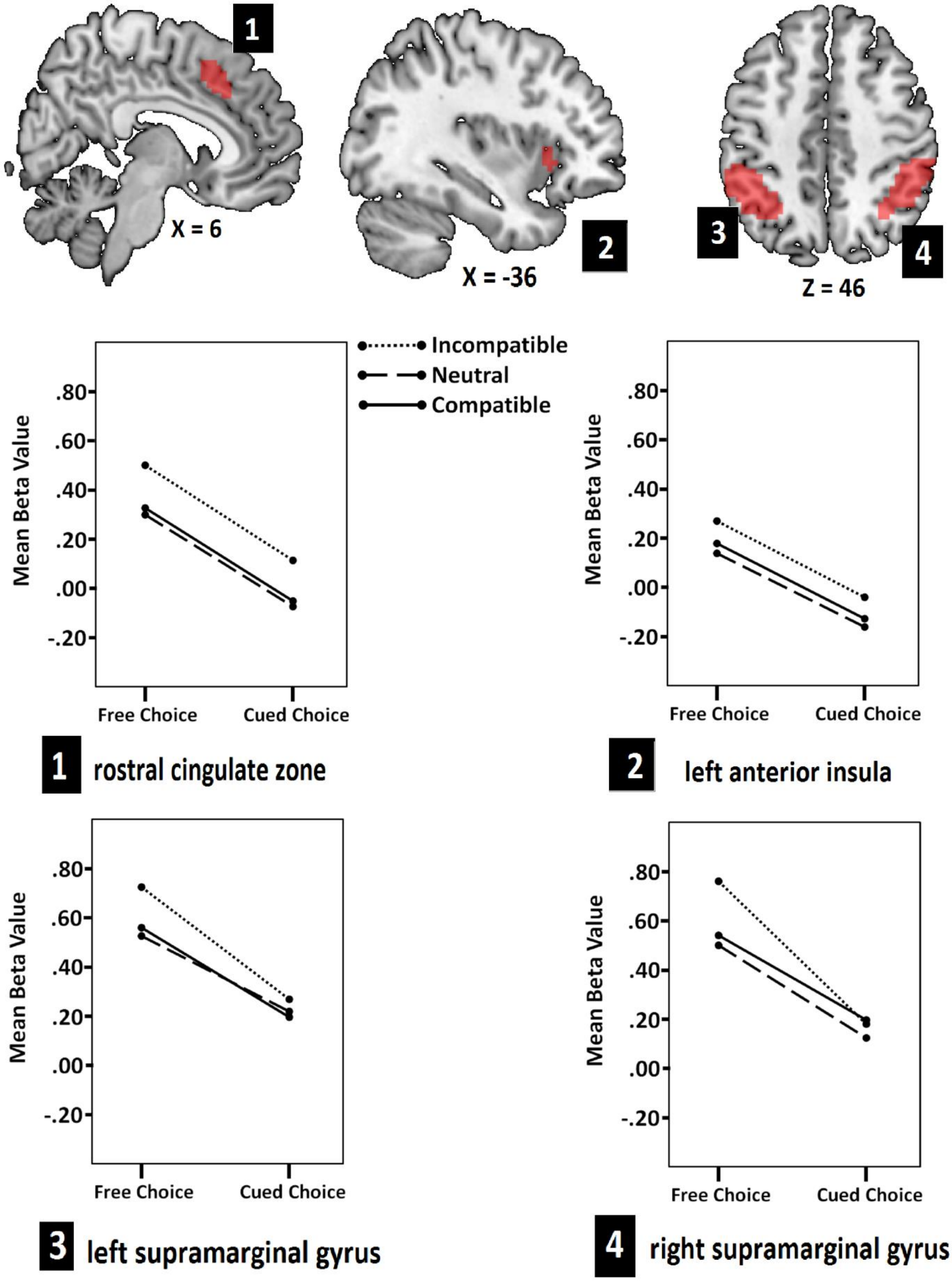

Figure 2. Areas that show a significant conflict activation pattern (incompatible significantly higher than compatible or neutral) on the whole brain level when contrasting free-choice related activation with cued-choice activation. The Y-axis depicts the beta values from the ROI. The peak-voxel coordinates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

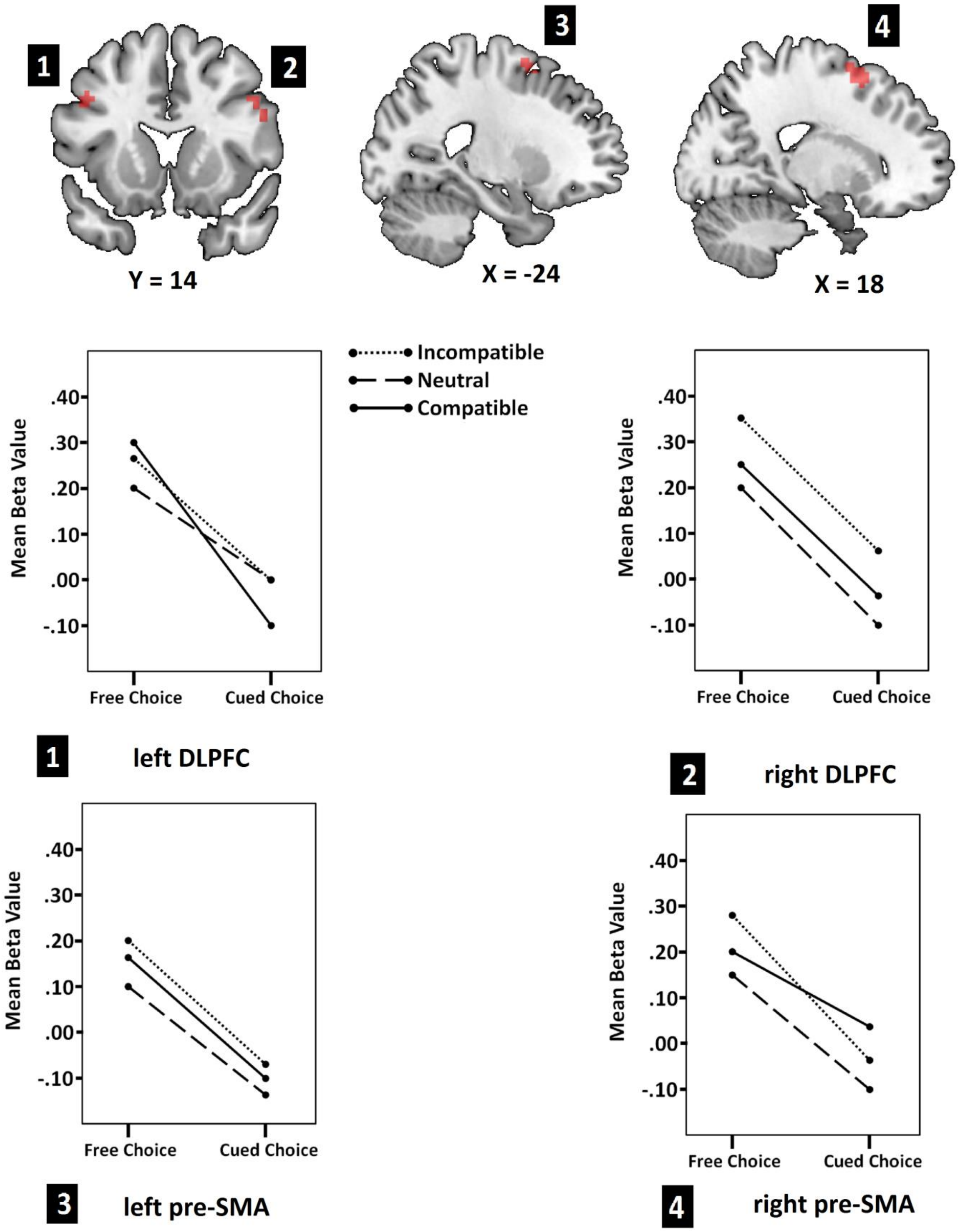

Figure 3. Areas that do not show a significant conflict activation pattern (incompatible significantly higher than compatible or neutral) on the whole brain level when contrasting free-choice related activation with cued-choice activation. The Y-axis depicts the beta values from the ROI. The peak-voxel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

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.

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.

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Chapter 2

The influence of subliminal primes on decoding response alternatives from cued- and free-choices[1]

In recent years mutli-voxel-pattern analysis (MVPA) has been increasingly used to successfully decode intentional choice from patterns of brain activity. This approach has deepened our understanding of the brain circuits involved in voluntary action. Recent studies have found that brain activity patterns in the frontopolar cortex and the precuneus both contain information that allows the decoding of voluntary choices. A question that remained unanswered is, however, whether these patterns of brain activity reflect the intentional choice or information that bias the choice process. To address this issue, we induced an unconscious bias with a metacontrast-priming manipulation. Using MVPA we decoded intentional choices and investigated how subliminal biases influence this decoding. We found that decoding accuracy in the precuneus, but not the frontopolar cortex, was influenced by unconscious biases indicating that decoding of intentional choices is susceptible to unconscious biases in the system. Additionally, we investigated whether we could decode choices from the RCZ and the anterior insula, two regions that have been related to intentional choice based on univariate analyses. We did not find evidence that these regions contained information about the choices participants made questioning their role in coding intentional choice.

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Introduction

Being able to make our own, voluntary choices is paramount to being human. It is not surprising then that understanding the neurocognitive mechanisms underlying voluntary choices has become a major research endeavor in cognitive neuroscience. A relatively new way to investigate the neurocognitive mechanisms of voluntary choice is by decoding choices from brain activity using multi-voxel pattern analysis (MVPA) (see e.g. Soon, Brass, Heinze, & Haynes, 2008; Haynes, 2011; Soon, He, Bode, & Haynes, 2013). MVPA uses local brain activity patterns to discriminate between different mental events (Haynes and Rees 2006; Norman, Polyn, Detre, & Haxby, 2006). In a seminal study Soon et al. (2008) used MVPA to investigate from which brain regions conscious choices can be decoded and whether decoding is possible before participants reported to become aware of the choice. Participants were asked to freely choose between pressing one of two buttons (Soon et al., 2008) when they felt the urge to do so. Soon et al. (2008) were able to decode voluntary choices from activation patterns in the frontopolar cortex, precuneus, pre-SMA and SMA. They thus concluded that it was indeed possible to decode unconscious intentions from brain activity that precedes awareness of these choices (Soon et al. 2008), similar to the results of the classical Libet experiment (Libet, Wright, & Gleason, 1982; Libet, Gleason, Wright, & Pearl, 1983). Based on the findings of Soon et al. (2008) it was assumed that conscious choices were preceded by brain processes that determined these choices. However, an alternative interpretation of the results suggests that it is not an unconscious intention that is decoded but rather an unconscious bias that influences the voluntary choice (Bode et al. 2014). The main aim of the current study was to investigate how unconscious biases affect decoding of response alternatives from brain activity. In order to do so, we reanalyzed a previous study by Teuchies and colleagues (2016) where an unconscious response bias was induced using subliminal priming (see e.g. Vorberg et al., 2003). Participants had to either freely choose which action to execute or were cued by a target stimulus. Before the target, a subliminal prime was presented that could be priming a left, a right or no response (when the prime was neutral and contained no directional information). Using univariate analysis, Teuchies et al. (2016) found that the RCZ and the anterior insula showed increased activation for incompatible trials when participants experienced a response conflict caused by subliminally presented primes. In the current study we analyzed these same imaging data using MVPA to investigate how an unconscious bias influences the decoding of response alternatives both in free-choice and in cued-choice trials. We wanted to investigate whether unconscious biases could influence the decoding accuracy from patterns of brain activity in areas that were identified by Soon and colleagues (2008). We hypothesized that the prediction accuracy would be higher in incongruent trials because in these trials participants have to overcome the response bias thereby making their intentional signal stronger. Furthermore, we predicted that the impact of congruency on free-choice trials should be stronger than in free-choice trials because in free choices participants had to overcome the bias by forming a strong intention while in cued trials it is sufficient to just act in accordance with the target, without the need of a strong intention (Waskom, Kumaran, Gordon, Rissman, & Wagner, 2014; Waskom, Frank, & Wagner, 2017).

The second aim of the current study was to test whether we could decode response alternatives from activity patterns in the RCZ and anterior insula which were found to be sensitive to subliminal priming in the univariate analysis of the same dataset (Teuchies et al., 2016). The RCZ has been implicated as one of the most crucial regions for intentional choice (Brass & Haggard, 2008). However, there is a controversy whether this region really codes the choice between different response alternatives or simply reflects differences in effort or task difficulty (Wisniewsky, Goschke, & Haynes, 2016).

Method Section

The data for the current study are the same data that were already described in detail in a previous study by Teuchies et al. (2016). The paradigm and the main findings of this previous study will be outlined briefly in the current paper. More detailed information regarding the paradigm, the experimental procedure and the behavioral data analysis can be found in Teuchies et al. (2016).

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.

Stimuli

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 superimposed by metacontrast masks of the same luminance (Figure 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.

Procedure

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. Participants were never alerted to the possibility of primes being presented, or influencing their behaviour. 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. Following the test phase, participants were explicitly told about the presence primes, and performed a prime-visibility test. 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. The responses to the primes were categorized using signal detection theory (Green & Swets, 1966). Measures of prime discriminability (d') for each participant were analysed.

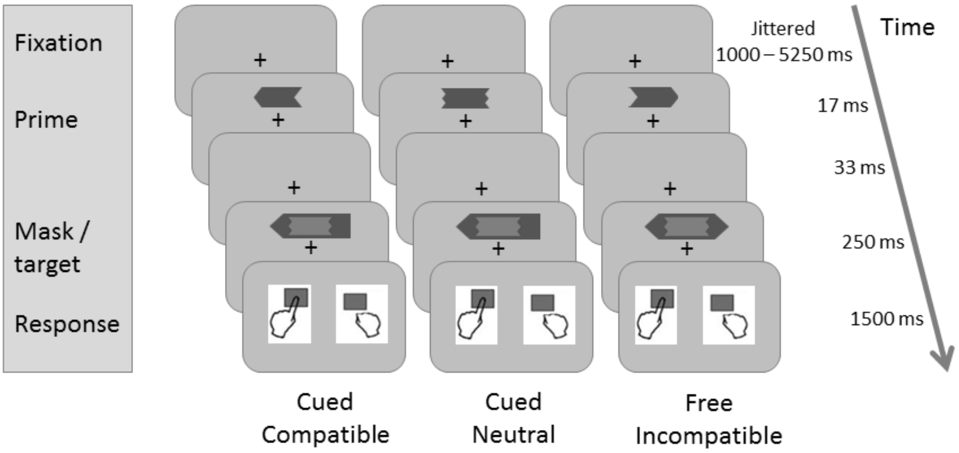

Figure 1. Schematic of trial procedure and stimuli, adapted from Wenke et al. (2010). Three example trials from the possible combinations of the factors choice type (cued: left and middle panel; free: right panel) and prime-action compatibility (compatible: left panel; neutral: middle panel; incompatible: 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.

fMRI data acquisition

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).

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).

First Level fMRI Analysis

During the preprocessing the first four functional images of each run were deleted as during the acquisition of these images the behavioral task was not yet running. The fifth functional image of each participant was then coregistered to the structural image of that participant. Next the structural image of each participant was coregistered to a standard T1 template available in SPM. The functional images were then corrected for differences in timing acquisition during slice timing and finally the images were corrected for movement during realignment. The images were left non-normalized and unsmoothed for the actual decoding analysis. The participant-level statistical analyses were performed using the general linear model (GLM) in SPM 8. Based on the response priming task 12 different regressors of interest were modelled (choice = cued/free X prime =

compatible/incompatible/neutral X response = left/right). 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 responses to 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.

Whole brain Multivariate fMRI Analysis

Whole brain multivariate fMRI Analyses were carried out using the PyMVPA toolbox (Hanke et al. 2009). We used a spherical searchlight with a radius of 3 voxels to find out which brain areas contained activity patterns that carry information about the direction of the response (left or right) participants made on each trial (Kriegeskorte, Goebel, & Bandettini, 2006). The first level β images used for the analysis were both non-normalized and unsmoothed. A linear support vector machine (SVM; cost parameter C = 1) was used for classification. In order to avoid problems of overfitting, we employed a leave-one-run-out cross-validation procedure. The classifier was first trained on the data of five runs and then tested on the remaining run. This process was repeated six times in order to use all possible combinations of training and test data. Classification accuracies were then averaged across all six iterations, resulting in one whole-brain image per participant per condition (compatible, incompatible or neutral for both free and cued-choices) containing the mean decoding accuracy for response direction. All decoding accuracies are reported relative to their respective chance levels (50%). Before carrying out the second-level analyses, all decoding maps were normalized and then smoothed with an 8 mm FWHM kernel.

Second level Analysis

On the whole brain level we used a flexible factorial design to look at the interaction between the factors choice (cued vs free) and compatibility (compatible vs incompatible). For this analysis we used four separate images (cued compatible and incompatible and free compatible and incompatible) per participant. These four images contained whole brain accuracy maps that were obtained during the whole brain decoding analysis. This allowed us to see whether there were any brain regions from which we could decode left or right responses better for compatible or incompatible trials and whether this made a difference for cued-choices and free-choices. Since we had strong a-priori expectations about which regions we expected to find and to increase sensitivity since regions in the prefrontal cortex show a significantly lower base rate for decoding than for instance regions within the visual sensory cortex (Bhandari, Gagne, & Badre, 2017), for the whole brain analysis we used a peak threshold of $p < 0.001$ (uncorrected for multiple comparisons in combination with a cluster threshold of 30 contiguous voxels).

Regions of interest analyses

In the region of interest (ROI) analyses we will look at closer both at the regions that show significant activation during the whole brain analysis as well as at some predefined ROI’s based on our previous study (Teuchies et al., 2016). We extracted the mean accuracies for each of the six conditions (cued compatible, incompatible and neutral and free compatible, incompatible and neutral) within these ROI’s per participant. The accuracy maps we used to obtain the mean accuracies were the output of the whole brain decoding analysis. Using predefined ROI’s we focused on the RCZ and the anterior insula. The RCZ and the anterior insula were the two regions in which activation seemed to be modulated the strongest by the subliminal primes. For the analysis an ROI with a radius of 5mm was created around the peak voxel of the region (RCZ MNI = [6 20 43]; Anterior insula MNI = [-36 20 -2]). For each ROI the accuracy values were 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 or interaction effect of choice (free vs cued) or 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. Finally, we will also look at activity in the motor cortex (MNI= [-42 -18 57] and [39 -18 57]) to validate our dataset. In the motor cortex we should be able to see relatively high decoding accuracies as this is the area where the actual left or right is implemented. The coordinates of the motor cortex are taken from the study by Soon et al. (2008).

Results

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). Mean reaction times (Table 1) 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. 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 show a significant compatibility effect, such that prime-compatible responses were significantly faster (*t*(25)

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

= 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).

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.

Whole brain decoding results

The whole brain decoding analysis did not reveal any of the brain regions found by Teuchies et al. (2016). We used a flexible factorial design including prime-response compatibility (incompatible/compatible) and choice (cued/free) as factors. The main effects of prime-response compatibility and choice revealed were not significant. Only the interaction contrast between prime-response compatibility and choice revealed a significant cluster of information in the right precuneus (MNI = [-6 -55 22]; *z*-score = 3.48; extent = 38 voxels). As shown in figure 2B this precuneus region overlaps with the precuneus region reported by Soon et al. (2008) [MNI [-12 -60 21]. We also did not find the frontopolar cortex to contain any information about the choices on the whole brain level.

Region of Interest (ROI) Analysis Results

Since we also found activation in the precuneus (MNI = [-6 -55 22]) at the whole brain analysis we also wanted to look at the accuracies per condition in this region (Figure 2). A 2x3 repeated-measures ANOVA (choice = cued/free x compatibility = compatible/incompatible/neutral) showed a significant interaction effect between choice and prime-response compatibility (*F*(2, 24) = 7.12, *p* = .004). We did not find any significant main effects of choice or prime-response compatibility. Using one-sample t-tests we determined whether the accuracies differed from chance level (50%). Apart from some random fluctuations around chance level, we expect no meaningful decoding accuracies below chance level, so here we used a one-tailed t-test to increase sensitivity. In the cued-choice conditions only the accuracy level of the compatible condition differed significantly from chance level (cued compatible: *t*(25) = 2.89, *p* = .004; cued incompatible: *t*(25) = -0.44, *p* = .332; cued neutral: *t*(25) = 0.50, *p* = .16). In the free-choice conditions only the accuracy level of the incompatible condition differed significantly from chance level (free compatible: *t*(25) = -1.43, *p* = .08; free incompatible:

t(25) = 1.95, *p* = .03; free neutral: *t*(25) = -0.71, *p* = .24). Using paired-samples t-tests (2-tailed) we then also assessed the difference between the compatibility conditions within the cued-choice and the free-choice conditions. The accuracy level from the compatible cued-choice condition (*M* = 55.0%) only differed significantly from the incompatible (*M* = 50%; *t*(25) = 2.56, *p* = .017) condition, but not from the neutral condition (*M* = 52%; *t*(25) = 1.11, *p* = .28). The accuracy levels from the compatible and the neutral free-choice conditions did not significantly differ (*t*(25) = -1.09, *p* = .28). The accuracy level from the incompatible free-choice condition (*M* = 54.0%) differed significantly from both the compatible (*M* = 47.4%; *t*(25) = -3.27, *p* = .003) and the neutral conditions (*M* = 47.8%; *t*(25) = 2.40, *p* = .024). The accuracy levels from the compatible and the neutral free-choice conditions did not significantly differ (*t*(25) = -.21, *p* = .83).

At the whole brain level we did not find the frontopolar cortex to contain information about the choices participants made. To see whether it truly was not possible to decode choices from this region we decided to create an ROI based on the coordinates reported by Soon et al. (2008) [MNI 0 60 -3]. A 2x3 (choice = cued/free x compatibility = compatible/incompatible/neutral) repeated-measures ANOVA showed no significant effects. In this ROI we did not observe any accuracies above chance level. We again used Bayesian one-sample t-tests (accuracy versus baseline) to check whether we could find evidence for a null-effect. The values of the Bayesian factors lay around 4, offering weak evidence in favor of the H0 hypothesis.

Based on our previous study (Teuchies et al., 2016) we also wanted to look how well we could decode choices in the RCZ and the anterior insula. A 2x3 repeated-measures ANOVA showed no significant effects in both the RCZ and the anterior insula. In the RCZ and the anterior insula we also observed no significant choice decoding above chance level, indicating that these two regions carried no information that allowed us to decode the left and right responses participants made. To test whether this lack of above chance level decoding was indeed a null-effect we performed a Bayesian one sample T-test (accuracy versus baseline) to see if we could find evidence in support of the H0 hypothesis. In the RCZ Bayes factors lay between 3 and 7 in support of the H0 hypothesis (no significant activation above chance level). In the anterior insula Bayes factors lay between 3 and 8 in support of the H0 hypothesis. This seems to indicate there is indeed a null-effect in these ROI's and thus supports our conclusion that the RCZ and the anterior insula carry no information with regard to the direction of the choice participants were going to make.

Finally, as a means to check the validity of the data-set we also looked at the decoding accuracies in the motor cortex. Decoding left and right choices from the motor cortex seems trivial and therefore should yield relatively large decoding accuracies. In both motor cortex ROI's we observed decoding accuracies that are well above chance level, ranging from 9% to 12% above chance level. These accuracies may seem not overly strong, but considering that the strongest decoding accuracies we observed are around 9% to 12% above chance level, the 5% above chance level accuracies we observed in other regions are not too bad in comparison. This may, however, not be too surprising. Decoding information from regions like the motor cortex or the visual cortex typically results in relatively high accuracy rates. Decoding from other brain regions on the other hand seems to be a lot harder and yields significantly lower base rates of information (Bhandari, Gagne, & Badre, 2017). Also, despite the fact that the current study should have sufficient power (*n* = 26, 6 runs with 144 trials each), the signal-to-noise ratio still seems to be low. A clear explanation as to why this is the case we cannot give, but it may be due to the design of the task for instance. Visual tasks that yield high decoding accuracies use a design in which stimuli are presented many times in a well randomized order. In decision-making designs, especially voluntary decision-making, a perfect counter balancing and randomization of trials is hard to obtain, possibly leading to a lower signal-to-noise ratio (Cai, Schuck, Pillow & Niv, 2016).

In summary, we were able to decode compatible left or right cued-choices and incompatible left or right free-choices in the precuneus. We did not find above chance accuracies in the frontopolar cortex, the RCZ or the anterior insula.

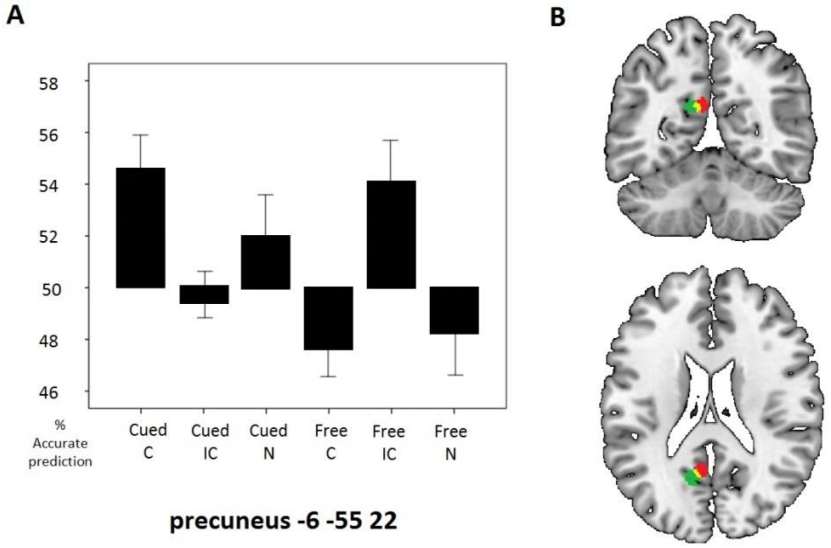

Figure 2. A) Decoding accuracies (above baseline = 50%) per condition (Cued C = cued compatible; Cued IC = cued incompatible; Cued N = cued neutral; Free C = free compatible; Free IC = free incompatible; Free N = free neutral) in the three precuneus ROI's. The precuneus [MNI -6 -55 22] was obtained during the whole brain analysis of the current study. B) Location of the precuneus found in the current study (red) and by Soon et al. (2008; green). The overlap is shown in yellow.

Discussion

In the current study we investigated whether decoding of response alternatives was sensitive to unconscious biases, as suggested by Bode et al. (2014). Furthermore, we compared the influence of such biases in free-choices and cued-choices. Our results indicate that the precuneus, a region that has been previously implicated in maintaining intentions to act (Soon et al., 2008; 2013; den Ouden, Frith, Frith, & Blakemore, 2005; Cavanna & Trimble, 2006) was sensitive to subliminal primes. As predicted, in the free-choice condition decoding accuracies were highest for incongruent trials, compared to both congruent trials and neutral trials. This is in line with previous research which suggested that in order to make an incongruent choice, participants have to make a greater effort to overcome the prime (Furstenberg, Breska, Sompolinsky, & Deouell, 2015; Waskom et al., 2017) leading to a stronger representation of the chosen response alternative. Interestingly and in contrast to our prediction, decoding accuracy was also high in the congruent cued-choice condition. Furthermore, we found no decoding accuracies above chance level in frontopolar cortex, indicating that this region contained no information that allowed the decoding of either cued-choices or free-choices in the current paradigm.

A second goal of the current study was to investigate whether it was possible to decode response alternatives from the RCZ and the anterior insula, two regions that have been found to play an important in role in voluntary decision making (Forstmann, Brass, Koch, & von Cramon, 2006; Demanet et al., 2013; Wisniewski, Reverberi, Tusche, & Haynes, 2015; Teuchies et al., 2016). The results revealed that in the RCZ and the anterior insula decoding accuracies were not above chance level further questioning the role of the RCZ in processing intentional choices.

Decoding intentional choices from the precuneus

The precuneus region we found in our whole brain analysis [MNI -6 -55 22] overlaps with the precuneus region reported by Soon et al. (2008) [MNI -12 -60 21]. Looking at the ROI results we found an interaction pattern between the decoding accuracies of the different choice conditions. In the free-choice condition the highest decoding accuracy was found in the incongruent trials. By contrast, in the cued-choice condition the highest decoding accuracy was found in congruent trials. While we had expected the pattern of results in free-choice trails and an interaction with cue-type, we did not expect a reversal of the pattern in the cued-choice condition. Exactly why we found this interaction pattern is hard to explain. We think it is likely that the decoding accuracies in these particular conditions were highest due to a combination of the task design and the strength of the proximal intentions of the participants, i.e. intending to perform an action and then immediately executing it (Furstenberg et al., 2015). Soon et al. (2008) argued the precuneus was involved in the storage of a decision until it reached awareness and could be executed. Based on our findings, and further speculating about the role of the precuneus, we believe that beyond storing the decision, the precuneus might integrate information from different sources that accumulates into the actual decision, which is then maintained in the precuneus until the decision is executed. In the current task choices were influenced by external sources such as the prime and the target and internal sources such as the intentions of the participants. The latter is especially relevant in the free-choice condition where participants do not have a target to cue their responses. Instead, in the free-choice trials participants had to endogenously decide for themselves which response to choose. The catch here was that they could not decide before the target was shown, because only then did they know whether a trial was a cued-choice trial or a free-choice trial. In a free-choice incompatible trial, participants had to overcome the interference caused by the primes. According to Furstenberg et al. (2015) the primes would have induced motor activation and formed an early neural bias in its direction. This unconscious response tendency can then be endogenously overcome by a voluntarily chosen response direction in a process called change of intention. This process would have taken some effort to execute and would have accumulated in a stronger intentional signal in favor of the chosen response option, making it easier for the MVPA classifier to decode the response in the incompatible free-choice condition. On the other hand, if participants chose to go with the prime, they did not need to form a strong intention or to invest a lot of effort because only one response option was activated which they could execute without competition (see e.g. Furstenberg, 2015). In the free-choice neutral condition there was no prime information influencing the choices so participants could also go with whatever response they felt like giving without much effort. This means the proximal intention to choose voluntary might be weaker in these conditions and the signal-to-noise ratio lower, making it harder for the MVPA to differentiate between left and right choices in these conditions.

In the cued-choice condition we found an unpredicted pattern of results. We observed higher decoding accuracies for the cued-compatible and cued-neutral conditions compared to the cued-incompatible condition, which is the opposite of what we observed in the free-choice condition. We expected a similar pattern as in the free-choice condition, only weaker because we thought cued-choices would not have needed strong intentions to carry out. At the moment we can only speculate about the inversion of the congruency effect in the cued condition. Based on the idea that the precuneus integrates all information that determines a specific response alternative, it is plausible to assume that the target provides a strong contribution to this integration process. In the cued-choice condition proximal intentions were always prompted exogenously by the target and not by an intentional choice, making these trials intrinsically different from free-choice trials. In the compatible and neutral condition the target provides a very strong signal to carry out a specific response which makes it easy to decode this signal. In the incompatible condition, the prime first activates response alternative A, followed by the target cueing response alternative B. Because both response alternative A and B are activated at the same time (Furstenberg et al., 2015), it is more difficult to accurately decode the selected response alternative. What makes this condition different from the free-choice incompatible condition is that here participants did not have to generate a strong intentional signal to overcome the primed response alternative but simply have to rely on the target. In short, we believe that accumulated information from the prime and the target sources would have led to a stronger proximal intention and a better signal-to-noise ratio in the cued-compatible and cued-neutral conditions compared to the cued-incompatible condition, while in free choice trials the opposite is the case.

A model that is often used to explain the decision-making process is drift diffusion, in which the evidence for two alternatives accumulates, is integrated over time and then compared to a fixed decision boundary (Gold & Shadlen, 2007; Ratcliff, 1978). Based on the findings of the current study we think it is possible that this accumulation of evidence from various sources such as external cues (mainly in the cued-choice condition) or internal intentions (mainly in the free-choice condition) takes place in the precuneus. This accumulation would continue until a certain threshold is reached and a decision is made which can then be immediately executed (as in the current study) or stored until the participant decides to act (as in the study by Soon et al., 2008).

Decoding intentional choices from the frontopolar cortex

In the current study we were not able to decode choices from activity patterns in the frontopolar cortex. According to Soon et al. (2008) the frontopolar cortex was the first cortical stage at which an actual decision was made. The precuneus on the other hand was thought to be involved in the storage of the decision until it reached awareness. This means that in the precuneus the information regarding the decision would be available almost until the point where the decision was actually carried out. In the frontopolar cortex, on the other hand, the information about a choice would be available some time before the decision was carried out. Considering the fact that in the current study we were decoding decisions at the time of the response, it is possible that by that point in time the information was no longer available in the frontopolar cortex, but was still there in the precuneus.

Differences between Soon and our study

The implications of our findings might be that in the study by Soon et al. (2008) the precuneus could indeed have been sensitive to some form of decision bias. Of course there are substantial difference between the current study and those by Soon et al. (2008). Soon et al. (2008) used a task that was based on the Libet task (Libet et al., 1982; 1983) where participants could decide when to make a voluntary action on their own pace. In the current study we wanted to deliberately introduce an unconscious bias using a response priming paradigm (Vorberg et al., 2003; Teuchies et al., 2016). This means that we were limited in the time window between the bias (prime) and the response. The reason here is that if the time between the prime and the response increases the effect of the prime might reverse into a negative compatibility effect (Eimer, 1999; Eimer & Schlaghecken, 1998, 2001, 2002; Eimer, Schubö, & Schlaghecken, 2002; Schlaghecken & Eimer, 2000, 2001, 2002, 2004) thus having the opposite effect than the one we intended. This means that we were unable to decode as far before the response as Soon et al. (2008) did (up to 8 seconds before the response was made). In the current study we were confined to look at effects occurring within the time window between the onset of the prime and the response (around 400 ms).

Decoding choices from the RCZ

Another important result of the current study relates to the decoding of the response alternative from the RCZ. In the current study we were not able to decode choices from activity patterns in the RCZ. This region was found to be sensitive to subliminal priming (Teuchies et al., 2016) and the RCZ has been implicated as an important region for intentional choices (Brass & Haggard, 2008). However, there is an ongoing controversy whether the RCZ truly processes the choice between different response alternatives or whether activity in the RCZ simply reflects differences in effort or task difficulty between experimental conditions (Wisniewsky et al., 2016). According to Fedorenko, Duncan, & Kanwisher (2013) activity in the RCZ might reflect more general preparatory processes that are related to voluntary choices but do not reflect processing of the choices themselves. One of these processes for instance that might play a role in the context of the current study would be conflict monitoring (see e.g. Botvinick, Braver, Barch, Carter, & Cohen, 2001). The findings of the current study offer support for the role of the RCZ in processing conflict or task difficulty rather than the actual choices as we were unable to decode choices from the RCZ. When analyzing the RCZ in the same dataset with univariate methods, the RCZ showed strong activation to incongruent trials, where conflicting response options were activated (Teuchies et al., 2016). Of course, MVPA is a different method than univariate fMRI analysis, so it is not straightforward or trivial to find the same regions when using both methods (Davis et al., 2014). The benefit of MVPA over conventional univariate fMRI analysis is that it is more sensitive as it does not require spatial averaging of individual voxels (Norman et al., 2006). If anything, this actually might offer further support for the interpretation that the RCZ is not involved in the actual decision making process. Despite the increased sensitivity of MVPA we do not find any evidence that the RCZ does somehow contain information about the actual choice somebody is about to make, which is in line with findings by previous studies (Wisniewski et al., 2015; Loose, Wisniewski, Rusconi, Goschke, & Haynes, 2017). It also has to be noted that despite the advantages and the increased sensitivity of MVPA the effects we found in the current study were very small. We were only able to correctly decode incompatible free-choices in 54% of the cases. Although the accuracy differences between the incompatible free-choice condition on the one hand and the compatible and neutral free-choice conditions on the other hand are significant, the accuracy levels are still not that much above chance level. This also means that we have to remain cautious when drawing conclusions from the results of the current study.

Conclusion

To conclude, the current study demonstrates that unconscious biases influence decoding accuracy in areas that have been previously related to intention formation, suggesting that unconscious biases might contribute to previous results. Furthermore, this influence completely reverses when comparing free and cued choices. The pattern of results suggests that the precuneus might be implicated in integrating external and internal signals that lead to a specific response. Furthermore, we were not able to decode intentional choices from the RCZ a region that has been implicated in intentional choice. This suggests that RCZ activation in univariate analyses might reflect general differences between conditions such as effort.

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Chapter 3

Reducing Belief in Free Will Increases the Impact of Subliminal Information While Making Free Choices[1]

The ability to make free choices is closely related to the concept of free-will. While we have the impression that we are in control of our choices they are also determined by external factors. Little is still known about the interaction between high-level beliefs about free-will and external factors influencing our choices. In the current study we investigated whether questioning beliefs in free-will leads to stronger unconscious influences on our choices. We combined the anti-free-will-belief manipulation with a subliminal response priming paradigm to bias free and cued choices. We observed a significant decrease in free-will belief in the anti-free-will group. This group showed an increased susceptibility to subliminal primes compared to the control group. This effect was only visible for free-choices, not for cued-choices suggesting that cued-choices are less susceptible to the manipulation. The results indicate that reducing top-down control leads to increased influences of external factors on voluntary behavior.

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[1] Teuchies, M., Demanet, J., & Brass, M. (In review). Reducing Belief in Free Will Increases the Impact of Subliminal Information While Making Free Choices. *Consciousness and Cognition.*

Introduction

The ability to freely choose between different alternatives is a fundamental aspect of human behavior and is central to the belief in free will which can be defined as the conviction that one determines one’s own outcomes (Vohs & Schooler, 2008). While the existence of free will has been questioned by philosophy for centuries, a majority of the people strongly feel that they have control over their behavior and thus have free will (International Social Survey Programme, 1998). Interestingly, the conviction that we are self-determined conflicts with a wealth of empirical research demonstrating that voluntary behavior can be influenced by all kinds of external factors, even if presented subliminally (Vorberg et al., 2003; Bargh et al., 2001; Arrington & Logan, 2005; Wenke, Fleming & Haggard, 2010; Orr & Weissman, 2011; Orr, Carp, & Weissman, 2012; Demanet, De Baene, Arrington, & Brass, 2013; Orr & Banich, 2014; Teuchies et al., 2016). This raises the fundamental question how our belief in free will interacts with such unconscious influences on our behavior. Recently, it has been demonstrated that belief in free will can be manipulated relatively easily by using text manipulations (Vohs & Schooler, 2008; Baumeister et al., 2009). A number of studies have demonstrated that questioning belief in free will leads to behavioral changes (see e.g. Vohs & Schooler, 2008; Baumeister, Masicampo, & Dewall, 2009; Alquist, Ainsworth & Baumeister, 2013; Protzko & Schooler, 2016). In seminal studies of Vohs and Schooler (2008) and Baumeister et al. (2009), for example, one group of participants read a text stating that free-will is an illusion. Participants in this group displayed an increase in cheating behavior (Vohs & Schooler, 2008) and aggression and a decrease in prosocial behaviour (Baumeister et al., 2009). Furthermore, it has been demonstrated that this anti-free-will belief manipulation also affects basic cognitive processes and their neural correlates (see e.g. Rigoni, Kühn, Sartori, & Brass, 2011; Rigoni, Kühn, Gaudino, Sartori, & Brass, 2012; Rigoni, Pourtois, & Brass, 2015). Rigoni et al. (2011) found that reducing belief in free-will leads to changes in voluntary motor preparation as indicated by a reduced readiness potential. Using a go/nogo paradigm Rigoni et al. (2014) also showed that reducing belief in free-will lead to a decrease in error detection as indicated by a decreased error-related negativity, a neural marker of error detection. These findings show that reducing belief in free-will can influence intentional actions and voluntary behavior, even at preconscious stages of decision making. In the current study, we set out to investigate whether people’s belief in free will affects to what degree unconscious information influences our behavior. One of the cleanest ways to impose unconscious influences on behavior is by using subliminal priming (Vorberg et al., 2003; Eimer & Schlaghecken, 2003; Kiesel et al., 2006; Jaskowski, 2008; Wenke, Fleming & Haggard, 2010; O’Connor & Neill, 2011; Kiefer, Adams, & Zovko, 2012; Sidarus, Chambon, & Haggard, 2013; Stenner et al., 2014; Doyen, Klein, Simons, & Cleeremans, 2014; Parkinson & Haggard, 2014; Le Bars, Hsu, Waszak, 2016; Teuchies et al., 2016). Subliminal priming has been used to study unconscious influences on behaviour across different fields of psychology such as cognitive psychology (Vorberg et al., 2003; Kiesel et al., 2006; Wenke et al., 2010), cognitive neuroscience (Orr & Banich, 2014; Teuchies et al., 2016) and social psychology (Baumeister, Bratslavsky, Muraven, & Tice, 1998; Holland, Hendriks, & Aarts, 2005; Dijksterhuis, Bos, Nordgren, & van Baaren, 2006). Using subliminal response priming it has been shown that incompatible prime-response combinations (i.e. small left or right pointing arrow primes that go in the opposite direction as the left or right response given by the participants) lead to an increase in reaction times and error rates compared to compatible prime-response combinations (Vorberg et al., 2003; Wenke et al., 2010; Teuchies et al., 2016).

In the current study we combine a subliminal response priming paradigm (see also Teuchies et al., 2016) with a belief in free will manipulation. The subliminal response priming paradigm was adapted from a paradigm by Vorberg et al. (2003) and Wenke et al. (2010). In the original paradigm developed by Vorberg et al. (2003), choices were always explicitly cued, in the sense that participants had 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). In the current study such cued trials were mixed with trials on which participants can 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. These neutral primes allowed us to distinguish interference effects (costs of incompatible priming) from facilitation effects (benefits of compatible priming). The participants were asked to respond in a balanced and spontaneous way on free choice trials (Arrington & Logan, 2005; Demanet et al., 2013, Teuchies et al., 2016). We manipulated free will beliefs with an experimental manipulation similar to the one that has been used by Vohs and Schooler (2008). Participants were randomly assigned to one of two groups. In the anti-free-will group participants were asked to read a text stating that scientists have found that free will is an illusion. In the control group participants read a text about consciousness that made no mention of free-will at all.

We propose that by reducing belief in free-will we are reducing intentional involvement in the choices people are making (Rigoni et al., 2011). Such a reduction of intentional involvement should result in a larger influence from the subliminal primes. One possibility is that the manipulation affects both cued-choice and free-choice trials to the same degree. However, it could also be that we only see an effect on free-choice trials because in this condition responses are self-determined and should thus be more sensitive to a manipulation of free will belief. The neutral prime condition can be used to determine whether the free will belief manipulation primarily affects the facilitation effect or the interference effect. A larger facilitation effect would indicate that the belief manipulation facilitates the processing of unconscious information. By contrast, a larger interference effect would indicate that the belief manipulation compromises the ability to control interfering information (Demanet et al., 2015).

Materials and Methods

Participants

Participants in this study were 56 Dutch-speaking students at Ghent University (12 male, mean age = 22.48 years, SD = 3.18) 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 compensated ten euros for their participation.

Study 1 Stimuli

Stimulus presentation and response registration was done using Tscope software (Stevens, Lammertyn, Verbruggen, & Vandierendonck, 2006). To make sure the primes were shown for only one refresh rate the duration of the primes was set to 10 ms. The actual time the prime appeared on the screen was logged for each trial. The response priming task was the same as used in Teuchies et al. (2016). 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).

Study 1 Procedure

At the start of the experiment participants were given up to 5 minutes to read one of two passages from Crick’s book The Astonishing Hypothesis (1994): The anti-free-will group read a passage about how scientists now claim that free-will is an illusion; the control group read a passage on consciousness that made no mention of free-will. To encourage participants to read the material carefully, the instructor stated that a comprehension test would be administered at the end of the experiment. Both texts were translated into Dutch by a native speaker and were about one A4 page long. The anti-free-will text counted 644 words, while the control text counted 529 words. After reading the text, participants performed the response priming task. The priming procedure was similar to that used by Teuchies et al. (2016) (fig. 1). Participants were instructed to respond to the direction of the target arrows with their right and left index fingers using the 'A' and the 'L' keys of the computer keyboard. 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

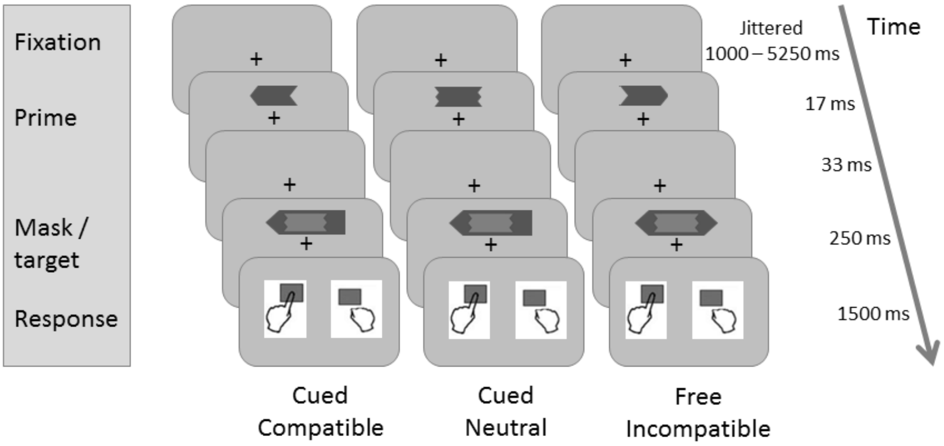

Figure 1. Schematic of trial procedure and stimuli, adapted from Wenke et al. (2010). Three example trials from the possible combinations of the factors choice type (cued: left and middle panel; free: right panel) and prime-action compatibility (compatible: left panel; neutral: middle panel; incompatible: 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.

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 1250ms. The task consisted of three 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 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. 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 Teuchies et al. (2016). 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. 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 analyzed. One week before the experiment as well as at the end of the experiment (but before the prime visibility test) we had participants fill out the Free Will Inventory (FWI) scale (Nadelhoffer, Shepard, Nahmias, Sripada, & Ross, 2014). This scale contains 15 statements and participants have to rate their agreement with each item on a 7-point likert scale (1 = ‘‘Strongly disagree”, 7 = ‘‘Strongly agree”). These 15 items are divided into three subgroups of five items each; the free will subscale (e.g., ‘‘People always have free will”, α = 0.80); the determinism subscale (e.g., ‘‘Everything that has ever happened had to happen precisely as it did, given what happened before”, α = 0.77); and the dualism subscale (e.g., ‘‘The human mind cannot simply be reduced to the brain”, α = 0.77).

Study 1 Results

Two 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 54 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’ = 0.055 ± 0.23; one-sample t-test, *t*(53) = 1.72, *p* = 0.09). A t-test further showed that d’ values did not significantly differ between the anti-free-will group (mean d’ = 0.070) and the control group (mean d’ = 0.040) (*t* (52) =0.452, *p* = .57).

Study 1 Free Will Inventory Scale

The total scores on the FWI scale showed a significant two-way interaction (group X pre-posttest measure) *F*(1, 52) = 4.15, *p* = .047. On the pre-test measure, both groups showed no difference in free-will belief (anti-free-will group: *M* = 64.14, *SD* = 9.17; control group: *M* = 63.96, *SD* = 10.63; *t*(52) = 0.041, *p* = .968). On the post-test measure the anti-free-will group had a lower score (*M* = 54.32, *SD* = 10.89) than the control group (*M* = 59.29, *SD* = 12.04). In both groups the scores are significantly lower on the post-test compared to the pre-test (anti-free-will group, *t*(26) = 4.68, *p* < .001; control group, *t*(26) = 3.45, *p* < .001). Looking at the difference between the two groups, the difference between the anti-free-will group and the control group was not significant (*t*(52) = 1.43, *p* = .16). Even though this difference is not significant, at least it shows a trend in the right direction.

Study 1 Behavioral Results

Mean reaction times (RT) for correct trials were determined as a function of choice type (free, cued), prime-response compatibility (compatible, incompatible or neutral) and group (anti-free-will or control group). The reaction times were submitted to a 2 X 3 X 2 repeated-measures ANOVA with choice type (cued and free) and prime-response compatibility (prime-response compatible vs. incompatible vs. neutral) as within-participants factors and group as between-participants factor. This analysis yielded a significant main effect of choice type (*F*(1, 52) = 55.14, *p* < .001) and prime-response compatibility, (*F*(2, 51) = 75.38, *p* < .001). The significant main effect of choice type indicates that responses in the cued-choice condition were faster (*M* = 419.3ms) compared to the free-choice condition (*M* = 445.8ms; *t*(53) = 7.41, *p* < .001, *d* = 0.46). The results (table 1) show a significant compatibility effect, such that prime-compatible responses were significantly faster (*M* = 418.5ms) compared to prime-incompatible responses (*M* = 449.6ms*;* *t*(53) = 12.30, *p* < .001, *d* = 0.51). Overall, directional primes led to a significant facilitation effect, such that prime-compatible responses were faster (*M* = 418.5ms) than prime-neutral responses (*M* = 429.6ms*;* *t*(53) = 7.07, *p* < .001, *d* = 0.16); as well as a significant interference effect, with slower prime-incompatible responses than prime-neutral responses (*t*(53) = -11.00, *p* < .001, *d* = 0.34). The three-way interaction between choice type, prime-response compatibility and group was significant (*F*(2, 51) = 4.12, *p* = .022). The main difference between the two groups can be found in the free-choice facilitation effect, i.e. the difference in reaction times between free-choice neutral and free-choice compatible trials. While there is no difference in the facilitation effect between the two groups for cued-choice trials, there is a significantly larger facilitation effect in the anti-free-will group compared to the control group for free-choice trials. In the control group there is no significant facilitation effect for the free-choice trials (4ms; *t*(26) = 1.06, *p* = .296, *d* = 0.05) and a significant facilitation effect for the cued-choice trials (15ms; *t*(26) = 7.70, *p* < .001, *d* = 0.29). In the anti-free-will group there is a significant facilitation effect for both the free-choice trials (15ms; *t*(26) = 4.57, *p* < .001, *d* = 0.28) and the cued-choice trials (11ms; *t*(26) = 4.71, *p* < .001, *d* = 0.17). The interference effects, i.e. the difference in reaction times between incompatible and neutral trials are similar in both groups for both cued-choice and free-choice trials (see table 1). In the control group the difference between cued incompatible and cued neutral trials is 12ms (*t*(26) = 4.72, *p* < .001, *d* = 0.21) and 29ms between free-choice incompatible and free-choice neutral trials (*t*(26) = 7.35, *p* < .001, *d* = 0.41). In the anti-free-will group the difference between cued incompatible and cued neutral trials is 13ms (*t*(26) = 4.98, *p* < .001, *d* = 0.22) and 26ms between free-choice incompatible and free-choice neutral trials (*t*(26) = 6.73, *p* < .001, *d* = 0.40).

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. In both groups participants chose the prime-compatible response option significantly more often (anti-free-will condition: 60.0%; control condition: 58.3%) than would be expected by chance (anti-free-will condition: *t*(26) = 9.96, *p* < .001; control condition: *t*(26) = 8.33, *p* < .001). The difference between the two groups is not significant *t*(26) = 0.77, *p* = .448). Looking at the error rates in the cued-choice condition we found no significant interaction between prime-response compatibility and group (*F*(2, 51) = 0.17, *p* = .851), indicating that the amount of errors did not differ between the anti-free-will group and the control group. There was a significant main effect for prime-response compatibility (*F*(2, 51) = 19.00, *p* < .001). Participants in both groups made significantly more errors on prime-incompatible trials (*M* = 10.3%) than on prime-compatible trials (*M* = 3.2%; *t*(53) = 6.27, *p* < .001).

Table 1. Reaction times and percentage of errors as a function of choice type, prime-action compatibility and group. Note: numbers in parentheses show standard deviations.

	Anti-free-will		Control group	
	Reaction time(ms)	% errors	Reaction time(ms)	% errors
Cued Choice				
Compatible	401.8 (5.8)	3.53 (3.0)	411.4 (5.6)	2.85 (2.5)
Incompatible	425.9 (5.9)	11.20 (8.6)	438.1 (5.2)	9.44 (8.2)
Neutral	412.8 (5.7)	5.81 (4.3)	426.1 (5.5)	5.09 (4.7)
Free Choice				
Compatible	417.3 (6.6)		443.5 (7.2)	
Incompatible	458.6 (6.3)		475.9 (7.1)	
Neutral	432.3 (6.1)		447.3 (6.6)	

Study 1 discussion

The results of study 1 indicate that reducing belief in free will leads to a stronger influence of unconscious information on free choice. Importantly, this influence was only observed for the facilitation effect of subliminal primes but not for interference. To increase the statistical power and reduce the likelihood of a false positive result, we added 65 participants to the first study. This way we ended up with a dataset containing data of 121 participants. The anti-free-will group contained

61 participants; the control group contained 60 participants. Power calculations using G*Power 3 (Faul, Erdfelder, Lang & Buchner, 2007) showed that such a sample size is sufficient to get 78% power to detect averaged sized effects. This also allowed us to compute correlations between the free will scores and the behavioral measures. All p-values reported for the pooled study have been corrected for multiple testing (i.e. the testing of the effect in the whole sample after testing in the first sample) using a Bonferroni correction by lowering the threshold for significance from p = .05 to p = .025. This way we would be able to further validate and interpret the results of the first study. Please note that this is a very conservative approach because we found a significant effect in the smaller sample already. Below the findings of the pooled studies are described.

Pooled Studies Materials and Methods

Pooled Studies Participants

Participants in the pooled studies were 121 Dutch-speaking students at Ghent University (23 male, mean age = 23.45 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 compensated ten euros for their participation.

Pooled Studies Stimuli and Procedure

The stimuli and procedures were identical to those used in study 1.

Pooled Studies Results

Six 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 d' values were not significantly different from zero (mean d' = 0.0025 ± 0.321; one-sample t-test, *t*(114) = 0.084, *p* = 0.933). A t-test further showed that d' values did not significantly differ between the anti-free-will group (mean d' = 0.0074) and the control group (mean d' = -0.0025) (*t* (113) =0.165, *p* = .86). One participant was excluded because of an error rate of 32% in the cued-choice trials.

Pooled Studies Free Will Inventory Scale Results

The total scores on the FWI scale showed a significant two-way interaction (group X pre-posttest measure) *F*(1, 110) = 7.01, *p* = .018. On the pre-test measure, both groups showed no difference in free-will belief (anti-free-will group: *M* = 63.26, *SD* = 8.49; control group: *M* = 63.30, *SD* = 10.85; *t*(112) = 0.025, *p* = .980). On the post-test measure the anti-free-will group has a lower score (*M* = 57.88, *SD* = 9.94) than the control group (*M* = 61.45, *SD* = 11.66). While in both groups the scores are lower on the post-test compared to the pre-test, this difference is only significant for the anti-free-will group (*t*(57) = 4.56, *p* < .001), not for the control group (*t*(55) = 1.67, *p* = .20). This indicates that the manipulation was effective in weakening beliefs in free will related to oneself in the anti-free-will group compared to the control group.

Pooled Studies Behavioral Results

Mean reaction times (RT) for correct trials were determined as a function of choice type (free, cued), prime-response compatibility (compatible, incompatible or neutral) and group (anti-free-will or control group). The reaction times were submitted to a 2 X 3 X 2 repeated-measures ANOVA with choice type (cued and free) and prime-response compatibility (prime-response compatible vs. incompatible vs. neutral) as within-participants factors and group as between-participants factor.

This analysis yielded a significant main effect of choice type (*F*(1,110) = 90.30, *p* < .001) and prime-response compatibility, (*F*(2, 109) = 177.29, *p* < .001). The significant main effect of choice type indicates that responses in the cued-choice condition were faster (*M* = 411.8ms) compared to the free-choice condition (*M* = 431.3ms; *t*(113) = 9.01, *p* < .001, *d* = 0.33). The results (table 2) show a significant compatibility effect, such that prime-compatible responses were significantly faster (*M* = 407.8ms) compared to prime-incompatible responses (*M* = 438.6ms; *t*(113) = 19.11, *p* < .001, *d* = 0.48). Overall, directional primes led to a significant facilitation effect, such that prime-compatible responses (*M* = 407.8ms) were faster than prime-neutral responses (*M* = 418.2ms; *t*(113) = 9.81, *p* < .001, *d* = 0.17); as well as a significant interference effect, with slower prime-incompatible responses than prime-neutral responses (*t*(53) = 14.90, *p* < .001, *d* = 0.32). The three-way interaction (Fig. 2) between choice type, prime-response compatibility and group was significant (*F*(2, 109) = 5.63, *p* = .010). The main difference between the two groups can again be found in the free-choice facilitation effect, i.e. the difference in reaction times between free-choice neutral and free-choice compatible trials: in the control group there is no significant facilitation effect for the free-choice trials (4ms; *t*(55) = 1.56, *p* = .236, *d* = 0.04) and a significant facilitation effect for the cued-choice trials (14ms; *t*(55) = 7.11, *p* < .001, *d* = 0.22). In the anti-free-will group there is a significant facilitation effect for both the free-choice trials (14ms; *t*(57) = 6.52, *p* < .001, *d* = 0.23) and the cued-choice trials (10ms; *t*(57) = 4.81, *p* < .001, *d* = 0.16). The interference effects, i.e. the difference in reaction times between incompatible and neutral trials are similar in both groups for both cued-choice and free-choice trials (see table 2). In the control group the difference between cued incompatible and cued neutral trials is 13ms (*t*(55) = 5.46, *p* < .001, *d* = 0.22) and 28ms between free-choice incompatible and free-choice neutral trials (*t*(55) = 9.76, *p* < .001, *d* = 0.37). In the anti-free-will group the difference between cued incompatible and cued neutral trials is 15ms (*t*(57) = 8.43, *p* < .001, *d* = 0.28) and 25ms between free-choice incompatible and free-choice neutral trials (*t*(57) = 8.21, *p* < .001, *d* = 0.42).

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. In both groups participants chose the prime-compatible response option significantly more often (anti-free-will group: 60.34%; control group: 60.23%) than would be expected by chance (anti-free-will group: $t(57) = 10.47$, $p < .001$; control group: $t(55) = 10.26$, $p < .001$). The difference between the two groups is not significant $t(112) = 0.08$, $p = .936$). Looking at the error rates in the cued-choice condition we found no significant interaction between prime-response compatibility and group ($F(2, 111) = 0.21$, $p = .979$) indicating that the amount of errors did not differ between the two groups. There was a significant main effect for prime-response compatibility ($F(2, 111) = 57.37$, $p < .001$). Participants in both groups made significantly more errors on prime-incompatible trials (M = 13%) than on prime-compatible trials (M = 4.5%; $t(113) = 10.81$, $p < .001$).

Table 2. Reaction times and percentage of errors as a function of choice type, prime-action compatibility and group. Note: numbers in parentheses show standard deviations.

	Anti-free-will		Control group	
	Reaction time(ms)	% errors	Reaction time(ms)	% errors
Cued Choice				
Compatible	397.3 (5.5)	4.06 (3.7)	401.2 (6.2)	4.94 (3.8)
Incompatible	422.4 (5.5)	12.68 (8.5)	428.2 (6.1)	13.28 (10.7)
Neutral	406.9 (5.5)	7.08 (4.9)	415.1 (6.5)	7.78 (6.4)
Free Choice				
Compatible	409.7 (6.5)		423.4 (7.6)	
Incompatible	449.4 (6.6)		454.7 (7.6)	
Neutral	424.0 (6.1)		427.2 (7.4)	

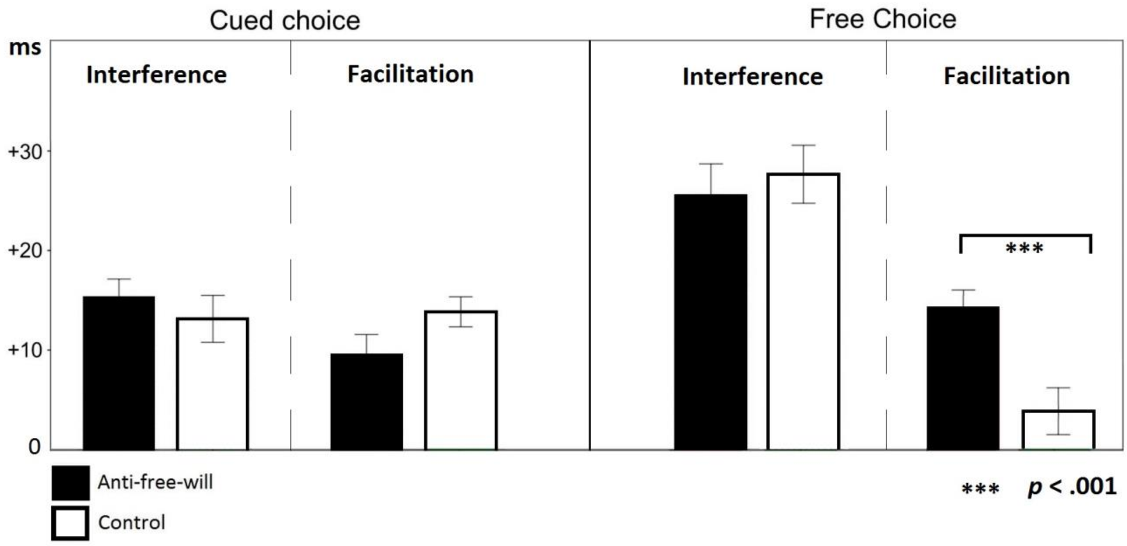

Figure 2. Reaction times (ms and standard errors) of the pooled data from studies 1 and 2 in terms of facilitation (difference between compatible and neutral reaction times) and interference (difference between incompatible and neutral reaction times; striped pattern) for the anti-free-will group (black) and the control group (white) for both cued-choices and free-choices.

Pooled Studies Correlations

The increased sample size allowed us to look at the correlations between the self-report measures and the behavioral measures. No significant correlations were found between any of the self-report measures and the behavioral measures.

General Discussion

The aim of the current study was to investigate how priming people with disbelief in free will alters unconscious influences on our behavior. We predicted that priming people with disbelief in free will should lead to an increased influence of unconscious information on behavior. Our results suggest that people that were primed with disbelief in free will are more strongly influenced by unconscious information. This effect, however, is restricted to the free choice condition.

The self-report measure shows that the anti-free-will manipulation was successful. Participants in the anti-free-will group showed a significant reduction in belief in free-will after the manipulation compared to the control group, in which belief in free-will did not differ before and after the manipulation. It has to be noted that this was only true for the pooled data from experiments 1 and 2, not for experiment 1 separately.

We argued that belief in free-will is a top-down influence on voluntary behavior because belief in free-will colors the perception participants have of the world (Vohs & Schooler, 2008). Believing that you are in control of the outcomes of your behavior also makes you more likely to feel intentionally involved in said behavior (Mueller & Dweck, 1998). We predicted that a reduction of belief in free-will would make participants in the anti-free-will group more susceptible to subliminal influences, as they might be less intentionally involved in the choices they had to make, especially voluntary choices. The anti-free-will belief manipulation seemed to have had an effect only on free-choice trials, not on cued-choice trials. Reaction times for cued-choices did not differ between the two groups and on cued-choice trials participants in both groups showed an equal amount of facilitation and interference caused by the primes. On free-choice trials we only observed an increased facilitation effect in the anti-free-will group, but not in the control group. This means that compared to a response to a neutral prime (a prime that carries no directional information) a prime-compatible response was made faster (i.e. the subliminal prime facilitated the response). This shows that while making free-choices participants in the anti-free-will group benefitted more from response-compatible primes compared to participants in the control group. Both groups showed an equal amount of interference, so the manipulation did not seem to have an effect on free-choices that were incompatible with the primes.

As hypothesized, the observation that only free-choices seem to be affected by the anti-free-will-belief manipulation might be related to the amount of intentional involvement participants have while making free-choices. The findings of the current study indicate that participants in the anti-free-will group were less intent on choosing freely, and thus were led more by the subliminal information on free choices, whereas people in the control group were intent more on choosing freely and were therefore less prone to follow the primes. Contrary to the free-choice condition, a minimum of intentional involvement is needed to make cued-choices. Participants simply have to follow the target arrows without having to intentionally make up their minds with regard to which response they want to choose. This reasoning is in line with findings from Wenke et al. (2010) who found that participants felt more control over the outcome of their choices when the proportion of free-choice trials was high compared to low. This means that participants were likely to feel more in control of their behavior when they could freely choose their actions, matching Vohs and Schooler's (2008) definition of free-will as “the belief that one determines one's own outcomes”. Looking at the literature, several studies have shown that the way subliminally presented information influences the response to a target stimulus largely depends on action intentions (Neumann, 1990; Ansorge, Heumann, & Scharlau, 2002; Ansorge & Neumann, 2005; Kiefer et al., 2012). Traditionally, subliminal processes were thought to occur independently of top-down control (Posner & Snyder, 1975; Schneider & Shiffrin, 1977). According to more recent studies subliminal, largely automatic, processes are more flexible and adaptable than the traditional views have led us to believe (Kiefer, 2007; Kiefer & Martens, 2010; Moors & De Houwer, 2006; Naccache, Blandin, & Dehaene, 2002; Neumann, 1990). Using the anti-free-will belief manipulation in the current study we believe we were able to influence action intentions of the participants in the anti-free-will group. Previous research on free will has already shown that this is possible. Reducing belief in free will increases conformity (Alquist et al., 2013), making participants rely more on external information to guide their behavior, which is what we expect the subliminal primes to do in the current study. Inducing disbelief in free will has also been shown to lead to reduced readiness potentials when participants had to prepare voluntary movements (Rigoni et al., 2011). Furthermore, Rigoni et al. (2011) showed that disbelief in free will affects intentional action even at a preconscious level of motor preparation, which presumably is also the level of motor preparation the subliminal primes are affecting.

Besides action intentions, Kiefer et al. (2012) showed that the currently activated task set also plays an important role in the processing of subliminal information. Given the nature of the anti-free-will belief manipulation (reading a text for 5 minutes) it is unlikely that participants in the anti-free-will belief group were completely deprived of their intention to respond freely on free-choice trials. The participants in the anti-free-will belief group also still responded slower on free-choice trials then on cued-choice trials, suggesting that some voluntary response processes were still taking place. Instead, the anti-free-will belief manipulation might have weakened the activation of the task set in such a way that responding freely on free-choice trials became less important to them, therefore making them respond more in a way that is similar to the cued-choice condition. Combining these findings we argue that in the current study the anti-free-will belief manipulation influenced participants' action intentions and task set activation and led them to be influenced more by the subliminal primes when making free choices.

Next to a difference between free-choices and cued-choices, in the current study we also saw a difference between how the anti-free-will-belief manipulation affects facilitation and interference caused by the subliminal primes. In the anti-free-will group we saw an increased facilitation effect for free-choice trials compared to the control group, but no increased interference effect, which did not differ between the two groups. This seems to suggest that the anti-free-will-belief manipulation made people more susceptible to compatible primes, but not more susceptible to incompatible primes. Why we only see an effect on facilitation and not on interference is not yet clear as we had expected the primes to influence both facilitation and interference. The finding that participants in the control group did not show a facilitation effect in the free-choice condition is in line with a previous study by Teuchies at el. (2016) that used the same subliminal priming paradigm. The question now is why we observed an increased facilitation effect in the anti-free-will group, an effect that usually seems to be lacking on free-choice trials? Unfortunately few other studies with subliminal neutral primes and free-choices have been reported. One other study that used a subliminal priming paradigm with neutral primes did not observe facilitation effects either, but only interference effects of the subliminal primes (De Pisapia et al., 2011). A possible explanation for the observed facilitation effect in the current study might be found in the self-inhibition hypothesis (Eimer & Schlaghecken, 1998; Schlaghecken & Eimer, 2002). According to this hypothesis masked subliminal stimuli automatically trigger a compatible response, which leads to facilitation effects when this response can be carried out immediately, but will be automatically inhibited when more time passes between the prime and the target. So, the longer the delay between prime and target, the stronger the inhibition becomes and could even lead to a reversal of the priming effects when the time between prime and target is sufficiently long (Eimer, 1999; Eimer & Schlaghecken, 1998, 2001, 2002; Eimer, Schubö, & Schlaghecken, 2002; Schlaghecken & Eimer, 2000, 2001, 2002). Schlaghecken and Eimer (2004) also observed this reversed (or negative) priming effect on free-choice trials. This suggests that the inhibition of a compatible response when the SOA between the prime and the target increases is not a perceptual process but rather a prime-induced state of motor activation that was observed in both cued-choice and free-choice conditions (Schlaghecken & Eimer, 2004). This observation might explain the findings of the current study. In the free-choice condition, the process of determining that the target is a double, bidirectional, arrow and then intentionally choosing a direction takes more time than in the cued-choice condition, where the target immediately dictates a response. The fact that it takes more time to come up with a response in the free-choice condition could lead to the process of response inhibition starting to take place. This would explain the similar reaction times for prime-compatible free-choices and prime-neutral free-choices in the control group. In the anti-free-will group, however, self-inhibition might be weakened due to the anti-free-will-belief manipulation making it easier for them to just go with the prime, resulting in the observed facilitation effect. This is in line with findings from a previous study that found a reduction in belief in free-will to be related to less self-control and inhibition (Rigoni et al., 2012). This explanation, however, is speculative and further research is needed to follow up on the current findings.

Why we did not observe a change in the interference effect in the anti-free-will group compared to the control group is also not clear. If the increased facilitation effect is indeed caused by less self-inhibition we would expect the interference effect to be affected in the anti-free-will group as well, as participants would be guided more by the external cues and less by their own intentions. In the current study, however, we do not observe a difference in the interference effect between both groups. One possible explanation could be that the slight increase in time between the prime and the response in the free-choice condition affects the facilitation of a response by a compatible prime more than the interference by an incompatible one. Looking at the data of Schlaghecken and Eimer (2000) it appears that a slight increase of the timing between the prime and the target leads to a steeper increase in reaction times on compatible trials compared to the decrease in reaction times on incompatible trials, meaning that it takes more time for the interference effect to be significantly reduced. This might explain why we observe a reliable difference between the groups on the facilitation effect but not on the interference effect. Of course, this is also speculation and further research is needed to see whether this is indeed the case.

Somewhat surprisingly, we observed no differences in the amount of prime-compatible free-choices participants in both groups made. In the current study both groups responded in a prime-compatible way in about 60% of the total amount of prime-compatible and prime-incompatible free-choice trials. Participants in the anti-free-will group just made their prime-compatible free-choices faster than participants in the control group. These results of the current study are in line with previous studies (Schlaghecken & Eimer, 2004; Kiesel et al., 2006; Wenke et al., 2010; Teuchies et al., 2016). Perhaps the instruction to try and respond in a random and balanced way is another top-down manipulation which is independent of the belief in free-will and stronger than the bottom-up influence, thereby somewhat reducing the effect of the manipulation and leading to similar results in both groups. Considering previous studies, however, the instruction to respond as random as possible on free-choice trials does not seem to make much of a difference when you compare the amount of prime-compatible responses from studies that do give this instructions with studies that do not. In both situations the reported amount of prime-compatible responses is about 59% of free-choice trials (Kiesel et al., 2006; Wenke et al., 2010).

Conclusion

In the current study we successfully reduced belief in free will and subsequently participants were more susceptible to the influence of subliminal primes, but only while making free-choices. Cued-choices seemed to be unaffected by the manipulation. Possible explanations for these findings are a reduction of intentional involvement while making free choices and a weaker task set activation. This seems to suggest that reducing our top-down involvement in making voluntary choices leaves more room for unconscious influences to guide and influence these choices. This finding suggests that subliminal influences on our behaviour are not fully automatic or uncontrollable, but can indeed be influenced by high-level beliefs. As this is one of the first studies that looks into the interaction between subliminal bottom-up influences and top-down influences on voluntary choices the results should be interpreted cautiously.

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Chapter 4

Search your feelings: Neural correlates of the subjective experience of fluency in action-selection in a subliminal response priming task[1]

In the current study we wanted to investigate the neural correlates of a particular type of metacognitive process, the subjective experience of fluency in action-selection. To manipulate fluency in action-selection we used a subliminal response priming paradigm. Participants then had to engage in the metacognitive process of rating how hard they felt it was to respond appropriately to the target stimuli. Participants rated incompatible trials during which subliminal primes were interfering with the correct response to be more difficult than trials on which primes facilitated the correct response. This increased sense of subjective difficulty was mirrored by increased activity in the rostral cingulate zone (RCZ) and the anterior insula, two regions that are functionally closely connected. The relationship between subjective ratings and activation in RCZ and anterior insula was still reliable when controlling for reaction times and prime-response compatibility. Our findings suggest that the metacognitive judgement of fluency in action-selection might be based on interoceptive signals resulting from increased effort possibly engaged by the RCZ.

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[1] Teuchies, M., Desender, K., de Baene, W., Demanet, J., & Brass, M. (In preparation). Search your feelings: Neural correlates of the subjective experience of fluency in action-selection in a subliminal response priming task.

Introduction

Imagine the cartoon situation where a little angel and a little devil are each sitting on one of your shoulders and are giving you opposite, but equally appealing advice. You probably would feel quite a bit of conflict when trying to figure out which advice to follow, although in this situation you have the luxury of actually knowing that two sources of opposing information are trying to influence you. Now imagine the little devil is invisible to you so you are unaware of its presence, but it is still able to get its advice through to you, subliminally. Could you still feel conflict in this situation? The chances are you could, you just would not now what caused your sense of conflict, but the fact that you can nevertheless feel it is the result of a process called metacognition, which refers to the subjective experiences that accompany our behavior (Metcalfe & Shimamura, 1994; Brown, 1978). In the current study we focused on one particular type of metacognitive process, namely the experience of fluency in action-selection (see e.g. Desender, Van Opstal, & Van den Bussche, 2014; Desender, Van Opstal, Hughes, & Van den Bussche, 2016). To manipulate fluency of action-selection we used a subliminal response priming paradigm to create a subliminal conflict between two response options. In the response priming task participants had to respond to left or right pointing target arrows that were preceded by subliminally presented prime arrows. Previous research using response priming has found that people respond slower and make more errors in the incompatible condition, in which the subliminal prime interferes with the correct response, compared to the compatible condition in which the prime facilitates the correct response (Vorberg et al., 2003; Eimer & Schlaghecken, 2003; Kiesel et al., 2006; Kouider, & Dehaene, 2007; Jaskowski, 2008; Van den Bussche, Van den Noortgate, & Reynvoet, 2009; Wenke, Fleming & Haggard, 2010; Furstenberg, Breska, Sompolinsky, & Deouell, 2015; Teuchies et al., 2016). It has also been shown that participants themselves can actually become aware of the impact of these subliminal stimuli on performance while being completely unaware of the stimuli themselves. For instance, participants experience more control over the outcome of an action when the outcome is produced by a prime-compatible response (Wenke et al. 2010; Chambon

& Haggard, 2012), and they rate incompatible trials (trials where the prime interfered with the response selection) as more difficult than compatible trials even if they were unaware of the presence of the primes (Desender et al., 2014; 2016; Questienne, Dijck, & Gevers,2017).

Previous research on subliminal conflict has shown that subliminal primes not only influence our behavior but also modulate activity in specific brain regions (Demanet, De Baene, Arrington, & Brass, 2013; Orr & Banich, 2014; Teuchies et al. 2016), most notably the rostral cingulate zone (RCZ) and the anterior insula. It was found that the RCZ and the anterior insula were activated more on incompatible trials, when subliminal primes interfered with the correct response, compared to neutral and compatible trials (Teuchies et al. 2016). The RCZ is part of the anterior cingulate cortex (ACC), which has often been linked to response competition and conflict monitoring (Kiehl et al., 2000; van Veen, Cohen, Botvinick, Stenger, & Carter, 2001; Botvinick, Braver, Barch, Carter, & Cohen, 2001; Barch, Braver, Sabb, & Noll, 2000; Cohen, Botvinick, & Carter, 2000; MacDonald, Cohen, Stenger, & Carter, 2000; Botvinick, Nystrom, Fissell, Carter, & Cohen, 1999; Carter, Braver, Barch, Botvinick, Noll, & Cohen, 1998; Carter, MacDonald, Botvinick, Ross, Stenger, Noll, & Cohen, 2000; Van Veen & Carter, 2002). The anterior insula has been linked to interoceptive awareness (see e.g. Craig, 2002; 2003; 2009). It has been suggested that high interoceptive sensitivity can be beneficial in guiding cognition and associated behavioural choices (Garfinkel & Critchley, 2013). People with better interoceptive sensitivity are thought to have better implicit memory for instance (Werner, Peres, Duschek, & Schandry, 2010) and display improved decision making on the Iowa Gambling Task (Dunn et al., 2010). Neuroimaging studies have found increasing activity in the anterior insula to be correlated with increasing task difficulty and ambiguity in decision-making contexts (Huettel, Song, & McCarthy, 2005; Feinstein, Stein, & Paulus, 2006; Singer, Critchley, & Preuschoff, 2009; Teuchies et al., 2016). The anterior insula has also often been found to be co-activated with the ACC (Cole & Schneider, 2007; Dosenbach et al., 2007; Craig, 2009; Gu, Hof, Friston, & Fan, 2013).

In the current study we wanted to investigate the neural correlates of the subjective experience of fluency in action-selection in a subliminal response priming task. Similar to previous studies (Desender et al., 2014; 2016) we asked participants after every trial how hard it was for them to respond as fast and as accurately as possible to the target arrows, thus obtaining a metacognitive judgement about the difficulty of the response that we could then correlate with brain activity.

Based on previous research (Desender et al. 2014; 2016) we expected that participants would rate incompatible trials to be more difficult than compatible and neutral trials. Based on previous fMRI studies (Teuchies et al., 2016; Demanet et al., 2014) we expected that activity in the RCZ would correlate with higher ratings of subjective difficulty, given that the RCZ has been found to be more active during trials that induce conflicting response options and these trials have been found to be more difficult to respond to (Desender et al., 2014; 2016). We also expected activity in the anterior insula to correlate positively with subjective difficulty because this region has also been found to show higher activation in the context of response conflict and because of the role it plays in interoceptive awareness (see e.g. Craig, 2002; 2003; 2009), which might play a crucial role in the subjective experience of difficulty. A second aim of the current study is to investigate whether brain activation correlated with subjective difficulty can be fully explained by reaction times or the conflict induced by the experimental manipulation (Desender, Van Opstal, & Van den Bussche, 2017).

Method Section

Participants

Participants in this study were 30 Dutch-speaking students at Ghent University (19 female, mean age = 23.77 years, SD = 3.20); 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 euros for their participation.

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 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. We logged the actual time the prime appeared on the screen for each trial. The mean presentation time was 18.00 ms (*sd* = 0.24). Three types of grey coloured primes were used: left or right pointing arrows or a neutral prime (which consisted of overlapping left and right pointing arrows). The primes were followed by superimposed metacontrast masks of the same luminance (see Fig. 1). The metacontrast masks were embedded within target arrows that pointed left or right. Primes subtended visual angles of 0.8° x 1.86°, and the targets 1.09° x 3.47°. Prime and target stimuli could appear randomly above or below a fixation cross at a visual angle of 1.38°. The unpredictable location was included to enhance the masking effect (Vorberg et al., 2003). A circular rating scale (fig. 1) was adapted from Kahnt, Heinzle, Park, & Haynes (2011). The x and y coordinates of the mouse response were converted into polar coordinates ranging from 0 degrees (most difficult) to 360 degrees (easiest). The thickness of the scale increased with difficulty. The easiest point on the scale was the tail of the circle; the most difficult point was the thickest point of the circle. The scale was rotated on every trial so that the starting point of the scale was never in a predictable place. This allowed us to prevent participants from preparing a motor response.

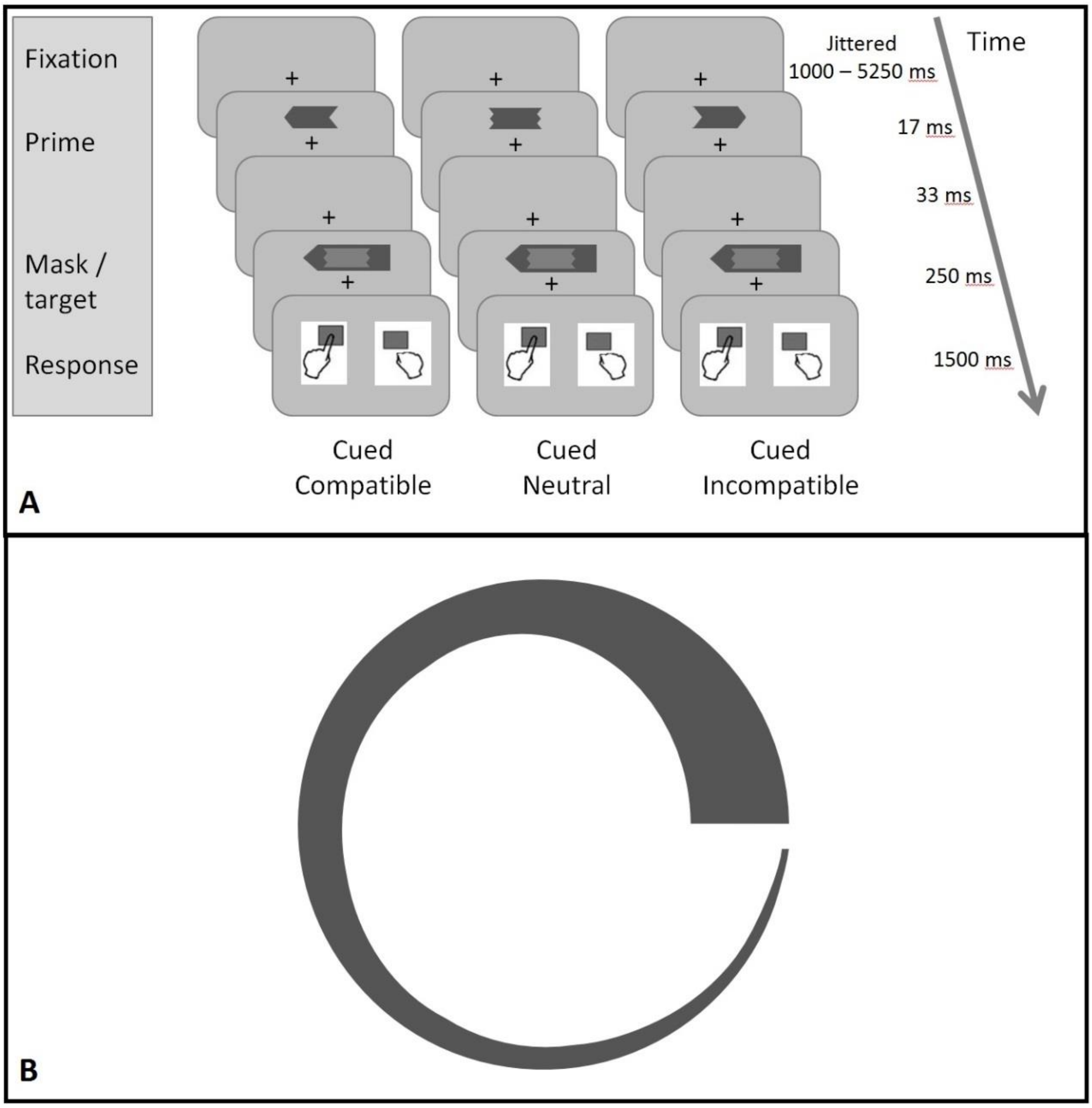

Figure 1. **A)** Schematic of trial procedure and stimuli, adapted from Wenke et al. (2010). Three example trials from the possible combinations of the factor prime-response compatibility (compatible: left panel; neutral: middle panel; incompatible: right panel). In each example, the participant responded 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. **B)** Circular rating scale adapted from Kahnt et al. (2011). The thin tail is the easiest point and the scale continuously increases in thickness and difficulty up to the thick end representing the most difficult point. Participants were instructed to use the whole scale and to click anywhere on the scale to express their subjective feeling of difficulty.

Procedure

Except for the rating phase, the priming procedure was similar to that used by Teuchies et al. (2016) (figure 1). Primes were presented for 16.7 ms, followed by a target that also functioned as a mask appearing with a stimulus onset asynchrony (SOA) of 32 ms. Target duration was 250 ms. The response window was set to 1500 ms. Participants were instructed to respond as fast and as accurately as possible to the direction of the target arrows with their left middle finger (left pointing targets) and left index finger (right pointing targets) using an MR compatible response box. If participants failed to respond within this time window, they saw “te laat” (too late) for 1000 ms after the trial. After each response a blank screen was shown for 1500 ms followed by the rating part of the trial during which the rating scale (fig. 1) was shown until participants had given their response. Once they clicked on the scale the screen went blank again for the inter-trial-interval. 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). Before doing the experiment in the scanner participants carried out two short training blocks of 48 trials each. In the first training block they were only presented with the response priming task, without the rating part. This was to let them experience the response priming task. When asked, all participants indicated that they made mistakes and that some trials indeed felt more difficult than others. In the second training block the rating part was added after every individual trial and participants were instructed to rate for each trial how difficult they found it to respond as fast and as accurate as possible to the target stimuli. Participants were never alerted to the possibility of primes being presented, or influencing their behaviour. The main task inside the fMRI scanner consisted of three blocks of 72 trials each. Within each block each prime-response compatibility condition (compatible, incompatible and neutral) occurred equally often. For the rating part of the trial participants were asked to indicate how difficult they found it to respond as fast and accurate as possible to the targets. With their right hand participants used an MR compatible optical track-ball mouse to select a point on the rating scale that matched their subjective sense of difficulty. Participants were instructed to use the entire scale and they were instructed that the extremities of the scale represented their personal most difficult or easiest points. At the end of the task participants were asked whether they noticed anything unusual about the stimuli during the task.

None of the participants noticed the primes, but three 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. 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. 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. A visual cue (‘*’) signaled when they were allowed to respond. The test consisted of two blocks of 50 trials each.

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.

Behavioral Data Analysis

Mean reaction times (RTs) and error rates were submitted to a repeated-measures ANOVA, with prime-response compatibility (compatible vs. incompatible vs. neutral) as factor. The subjective ratings were analyzed similarly. Ratings were submitted to a repeated-measures ANOVA, with prime-response compatibility (compatible vs. incompatible vs. neutral) as factor. The responses to the primes in the visibility check were categorized using signal detection theory (Green & Swets, 1966). Measures of prime discriminability (d’) for each participant were analyzed. We then used a one-sample t-test to see whether the mean d’ of the sample deviated from zero.

General GLM analyses

The participant-level statistical analyses were performed using the general linear model (GLM). Based on the design of the response priming task (compatible/incompatible/neutral), three different regressors of interest were modelled. In order to look at brain activation that could be uniquely attributed to subjective ratings or reaction times we added reaction times and subjective ratings as extra regressors of interest. Reaction times and ratings are not perfectly decorrelated (r = .017) so adding raw variables would not have given us the cleanest results. To obtain a cleaner picture of each of these variables contribution to the observed brain activation we used the residuals obtained from a linear regression either with reaction times as the dependent variable and subjective ratings as the independent variable or vice versa. The obtained residuals were now perfectly decorrelated with the predictor variable. The residuals were obtained for each participant separately. To visualize the effects of rating per compatibility condition, we also created a model were we performed a median split on the subjective rating data. This way we ended up with 6 regressors, compatible easy and difficult, incompatible easy and difficult and neutral easy and difficult, allowing us to directly contrast trials that were experienced as easy with trials that were experienced as difficult. We used this model for the ROI analysis, allowing us to look how brain activity differed between the 6 different conditions compatible easy and difficult, incompatible easy and difficult and neutral easy and difficult. Erroneous trials and the first trials of each block were always modeled as separate regressors of no interest (4.9% of the trials). 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. Using the first level model created with the binned subjective rating data we contrasted difficult trials versus easy trials. Using one-sample t-tests we also looked at the effects of the subjective difficulty ratings and reaction times across prime-response compatibility conditions. The subjective difficulty ratings and the reaction times had been added as parametric regressors during the first-level analysis. Only clusters significant at the familywise peak-level threshold of $p < .05$ are reported. The resulting maps were overlaid onto a structural image of a standard MNI brain, and the coordinates reported correspond to the MNI coordinate system.

Regions of interest analyses

In the region of interest (ROI) analyses, we focused on the RCZ and the anterior insula as these were our principal ROI's based on a previous study by Teuchies at al., 2016. To create ROI's we created spheres with a 5mm radius around the peak coordinates of the RCZ [MNI 6 20 43] and the anterior insula [MNI -36 20 -2]. Besides the ROI's based on previous studies we also looked at brain regions that showed significant activation in whole brain analysis. The percent beta change of each ROI was submitted to a 2 X 3 repeated-measures ANOVA, with factors subjective rating (difficult vs. easy) and prime-response compatibility (compatible vs. incompatible vs. neutral). When a significant main effect of subjective rating or 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.

Results

Behavioral Results

Main Task

Participants failed to respond during the 1500 ms response window on 0.6% of the trials. For the remaining data, mean reaction times (RT) for correct trials were determined as a function of prime-response compatibility (compatible, incompatible or neutral). The reaction times were submitted to a repeated-measures ANOVA with prime-response compatibility (prime-response compatible vs. incompatible vs. neutral) as factor. This analysis yielded a significant main effect of prime-response compatibility, ($F(2, 28) = 39.24$, $p < .001$, $\eta p^2 = .737$), such that prime-compatible responses (M = 426.8 ms) were significantly faster compared to prime-incompatible responses (M = 453.9 ms; incompatible – compatible = 27 ms; $t(29) = 7.94$, $p < .001$, $d = 0.68$). Prime-compatible responses were not faster than prime-neutral responses (M = 430.6 ms; neutral – compatible= 7ms; $t(29)$ = -

1.27, *p* = .22, d = 0.11), meaning that directional primes did not lead to a significant facilitation effect. There was however a significant interference effect, meaning that prime-incompatible responses were slower than responses to neutral primes (incompatible – neutral= 23ms; *t*(29) = -7.97, *p* < .001, *d* = 0.62). Looking at the error rates we observed a significant main effect of prime-response compatibility, (*F*(2, 28) = 12.53, *p* < .001, ηp^2 = .472). Participants made significantly more errors on prime-incompatible trials (*M* = 7.93%) than on prime-compatible trials (*M* = 2.92%; *t*(29) = 5.1, *p* < 0.001, *d* = 0.93) and on neutral trials (*M* = 3.84%; *t*(29) = 4.3, *p* < 0.001, *d* = 0.73). Participants made slightly more errors on neutral-prime trials than on prime-compatible trials but this difference was not significant (*t*(29) = -1.7, *p* = 0.1, *d* = 0.28).

For the subjective difficulty ratings we also observed a main effect for prime-response compatibility (*F*(2, 28) = 9.60, *p* < .001, ηp^2 = .407). Due to the circular nature of the scale ratings lie between 0 (difficult) and 360 degrees (easy). Participants rated prime-incompatible trials (*M* = 238.4) as significantly more difficult than prime-compatible trials (*M* = 248.7; *t*(29) = 4.1, *p* < 0.001, *d* = 0.20) and more difficult than neutral trials (*M* = 249.2; *t*(29) = -4.3, *p* < 0.001, *d* = 0.21). Ratings for neutral-prime trials did not differ from ratings for prime-compatible trials (*t*(29) = -2.9, *p* = 0.77, *d* = 0.01).

Finally, it has to be noted that in the current study reaction times and subjective ratings were correlated, but the correlation was not very strong (*r* = .17; the correlations were calculated for each participant separately, then we calculated the mean correlation after doing a Fisher Z transformation).

Prime visibility

The d’ values were not significantly different from zero (mean d’ = 0.077, *sd* = 0.37); one-sample t-test, t(29) = 1.13, *p* = 0.27). Given that d’ values should be as low as possible and would be zero in case of perfect invisibility, it can be concluded that all participants were unaware of the direction and the presence of the prime stimuli. We correlated the subjective ratings with the individual Dprime values, but we found no significant results, indicating that the subjective ratings were not influenced by any chance visibility of the primes.

We further carried out a multiple regression analysis with subjective rating as dependent variable and reaction times and d' as independent variables to see to what extent these factors could explain the subjective difficulty ratings. Although reaction times proved to be a significant predictor for subjective ratings (standardized beta = -.21, $p < .001$) the amount of variance explained is very low at just 4.5% ($R^2 = .045$). Adding d' did not improve the model fit. The amount of variance explains stays virtually the same at 4.6% ($R^2 = .046$) as d' is not a significant predictor for subjective ratings (standardized beta = 0.026, $p = .11$). This indicates that reaction times seem to count for only a very small amount when it comes to explaining the subjective ratings.

Table 1.

	Reaction time (ms)	% errors
Choice type: Cued Choice		
Compatible	426.8 (8.1)	2.92 (0.6)
Incompatible	453.9 (6.8)	7.93 (1.3)
Cued Neutral	430.6 (6.7)	3.84 (0.6)
	Subjective difficulty rating (degrees)	
Compatible	248.7 (9.5)	
Incompatible	238.4 (9.5)	
Neutral	249.2 (9.4)	

Reaction times and percentage of errors as a function of choice type and prime-action compatibility. The subjective difficulty ratings are reported in degrees on a scale from 0 – 359.
Note: numbers in parentheses show standard errors of the means across participants

fMRI Results

Whole-Brain Analysis Results

In the whole brain analysis we first looked for brain regions that showed significant activity that was correlated with subjective ratings and reaction times. We looked at both these measures, as reaction times and difficulty are thought to be closely linked (see e.g. Desender, Calderon, Van Opstal, & Van den Bussche, 2017). We wanted to see if subjective ratings and reaction times showed any unique and/or overlapping activation. As explained before, we used the residuals from a regression analysis to obtain measures of reaction times and subjective ratings. This way we could use the subjective rating data while controlling for reaction times and vice versa. On the whole brain level we then used one-sample t-tests to look at the effect of the subjective ratings and reaction times independent of prime-response compatibility (Table 2). The parameter of subjective ratings revealed significant clusters of FWE corrected activation in the RCZ [MNI 0 17 52] and the left anterior insula [MNI -39 20 1]. The left anterior insula cluster is closely located to the anterior insula [MNI -36 20 -2] reported by Teuchies et al. (2016). The parameter of reaction times revealed one significant FWE corrected

Table 2.

Region	Peak Coordinates (MNI)	*z*-score	Extent
Subjective Ratings			
rostral cingulate zone	0 17 52	5.86	17
Left anterior insula	-39 20 1	4.62	1*
Reaction Times			
left postcentral gyrus	-51 -34 52	4.84	8

Active regions on whole-brain level revealed using a 2nd level flexible factorial design, contrasting difficult trials with easy trials and one-sample t-tests looking at the effects of reaction times and subjective ratings.
(all regions cluster-level threshold *P* < .05, family-wise error correction, initial voxel level threshold T = 5.63, p < .001).
* the anterior insula cluster consists of 104 voxels when we looked at it using a more liberal threshold of p < .001 uncorrected).

cluster of activation in the left inferior parietal cortex [MNI -51 -34 52]. These results indicate that the RCZ and the anterior insula showed increased activity with increased subjective difficulty and that this activation could not be explained by prime-response compatibility or by reaction times.

Region of Interest (ROI) Analysis Results

To avoid double dipping issues, for the RCZ and the anterior insula we looked at ROI's (Figure 2) based on our previous study (Teuchies et al., 2016). During the whole brain analysis we found that activity in the RCZ increased when the ratings of the subjective difficulty increased, independent from prime-response compatibility and reaction times, as the parameter for subjective ratings was orthogonal to both these factors. Having found that subjective ratings increased activity independent of prime-response compatibility, we then used the GLM model based on the binned subjective ratings data (consisting of 6 regressors compatible easy; compatible difficult; incompatible easy – incompatible difficult; neutral easy – neutral difficult) to look at the effects of subjective difficulty and prime-compatibility. Teuchies et al. (2016) also found that the RCZ and the anterior insula showed a main-effect for prime-response compatibility, with the incompatible condition showing higher activation than the compatible and the neutral conditions. We also wanted to use the ROI analysis to see whether we could replicate the findings by Teuchies et al. (2016).

Rostral Cingulate Zone

As expected based on the whole-brain analysis we observed a main effect of subjective difficulty in the RCZ (MNI [6 20 43]; $F(1,29) = 9.974$, $p = 0.004$, $\eta^2 = .256$). Trials that were rated as more difficult caused higher activation than trials that were rated as easy ($t(29) = 3.16$, $p < .01$, $d = .30$). We observed no significant interaction between compatibility and subjective rating ($F(2,28) = 0.81$, $p = 0.46$, $\eta^2 = .055$). Replicating the findings of our previous study we also observed a main-effect of prime-response compatibility, ($F(2,28) = 4.53$, $p = 0.02$, $\eta^2 = .245$), showing that the RCZ was more strongly activated in the incompatible prime-response condition compared to the compatible condition ($t(29) = -2.64$, $p = .013$, $d = .28$) and compared to the neutral condition ($t(29) = 2.17$, $p = .04$, $d = .24$). The compatible and the neutral conditions did not differ in activation ($t(29) = -0.46$, $p = .65$, $d = .04$).

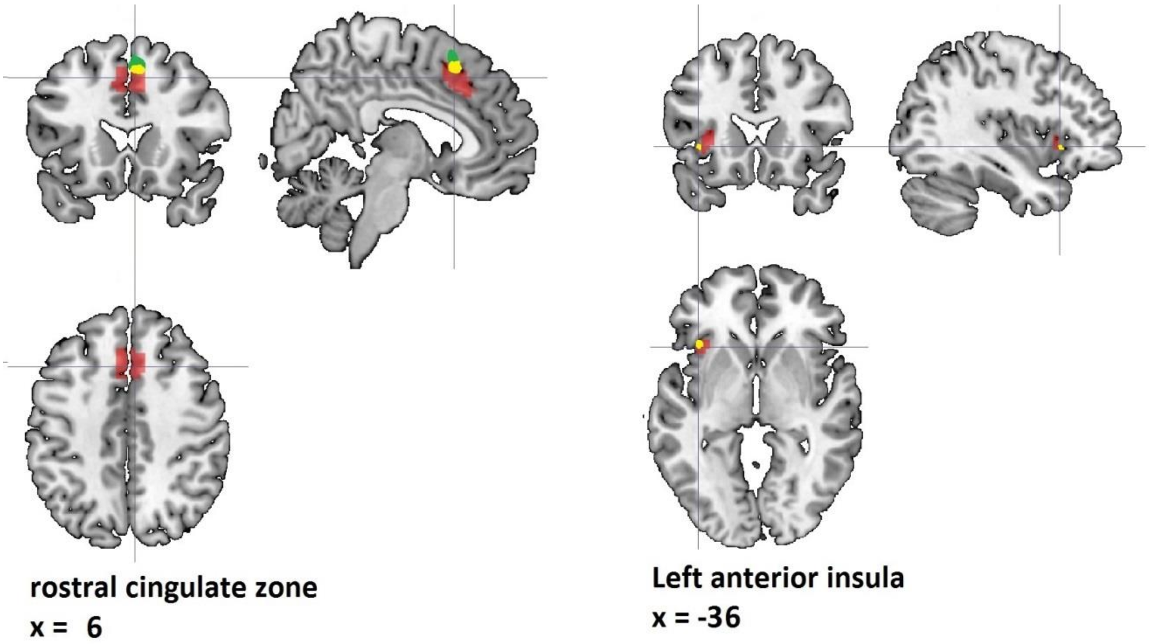

Figure 2. Main areas of interest that show higher activation when the sense of subjective difficulty increased independent from prime-response compatibility and after regressing out the effect of reaction times. A) **Rostral Cingulate Zone.** RED = peak coordinate [MNI 6 20 43] obtained from a previous study by Teuchies et al. (2016); GREEN = peak coordinate [MNI 0 17 52] obtained on the whole brain level when looking at one-sample T maps for the parameter of the subjective difficulty ratings; YELLOW = overlap B) **Left Anterior insula.** RED = peak coordinate [MNI -36 20 -2] obtained from a previous study by Teuchies et al. (2016); Yellow = overlap with Anterior insula [-39 20 1], obtained on the whole brain level when looking at one-sample T maps for the parameter of the subjective difficulty ratings. The subjective difficulty ratings were not added as raw data, but we used the residuals from a regression analysis in which we regressed the subjective difficulty ratings on the reaction times in order to filter out the influence of reaction times.

Anterior Insula

In the left anterior insula ROI [MNI -36 20 -1] defined by the results of Teuchies et al. (2016) we observed a main effect of subjective difficulty ($F(1,29) = 5.28$, $p = 0.029$, $\eta^2 = .154$). Trials that were rated as more difficult caused higher activation than trials that were rated as easy ($t(29) = 2.27$, $p = .031$, $d = .22$). We observed no significant interaction between compatibility and subjective rating

F(2,28) = 0.686, *p* = 0.51, η^2 = .047. Replicating our previous findings we also observed a main effect of prime-response compatibility, *F*(2,28) = 4.78, *p* = 0.016, η^2 = .255. This region was more strongly activated in the incompatible prime-response condition compared to the compatible condition (*t*(29) = -2.30, *p* = .029, *d* = .18) and the neutral condition (*t*(29) = 2.81, *p* = .009, *d* = .29). The compatible and the neutral conditions did not differ in activation (*t*(29) = -1.01, *p* = .32, *d* = .11).

Mediation analysis

In order to see how the anterior insula and the RCZ were co-activated we performed a mediation analysis and found that the relationship between activity in the RCZ and the subjective ratings was mediated by activity in the anterior insula (Figure 3). To do this we created a new first level GLM model in which every trial of the task is modeled by a separate regressor. This allowed us to obtain trial-by-trial beta values for the ROI's of the RCZ and the anterior insula obtained from our previous study (Teuchies et al., 2016) which we then correlated with the residuals for the subjective rating data that were also used in the whole brain analysis. As Figure 3 illustrates, activity in the RCZ was significantly related to both activity in the anterior insula (*β* = .65, *t*(6115) = 49.38, *p* < .001) and the subjective ratings (*β* = .017, *t*(6114) = 2.91, *p* < .01). Additionally, activity in the anterior insula was significantly related to the subjective ratings (*β* = .016, *t*(6114) = 2.91, *p* < .001). We tested the significance of the indirect effect using bootstrapping procedures. Unstandardized indirect effects were computed for each of 1000 bootstrapped samples. The total effect of the model is .028 (lower 95% CI .02 – higher 95% CI .037; *p* < .001). The ACME value is .011 (lower 95% CI .00 – higher 95% CI .017; *p* < .001). This shows that the estimated average increase in the subjective ratings as a result of the activity in the anterior insula is about 36% of the total effect that RCZ activity has on the subjective ratings. These data provide an indication that at least some of the information flow first passes through the RCZ, then through the anterior insula which leads to the subjective ratings.

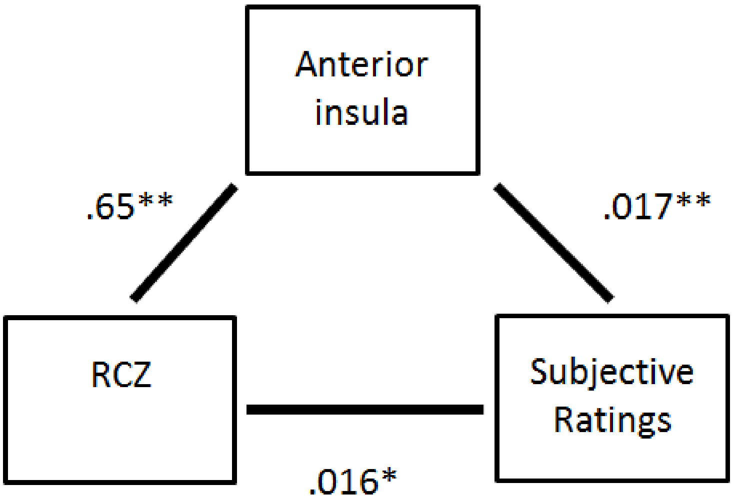

Figure 3. Standardized regression coefficients for the relationship between activity in the RCZ and the subjective ratings as mediated by activity in the anterior insula. * *p* < .01 ; ** *p* < .001

Discussion

In the current study we set out to see which brain regions correlated with the sense of subjective difficulty during action-selection and execution in a response priming task. The behavioral data showed that participants were slower and made more errors on incompatible trials (i.e., when subliminal conflicting information was present), compared to compatible and neutral trials where no conflicting information was present. Participants also rated incompatible trials to be more difficult to respond to despite the fact that they were unaware of the presence of the primes, as evidenced by the d’ values, which is in line with previous studies (Chambon & Haggard, 2012; Desender, Van Opstal, & Van den Bussche, 2014; Desender, Van Opstal, Hughes, & Van den Bussche, 2016). This indicates that participants were able to sense when conflicting information was making it harder for them to respond.

Imaging results

Looking at the imaging results, as hypothesized, the whole-brain analysis results showed that activity in the RCZ and the anterior insula correlated positively with subjective ratings, even when controlling for prime-response compatibility and the effect of reaction times. This indicates that we did indeed find the hypothesized brain activity in the RCZ and the anterior insula, but that neither reaction times, nor prime-response compatibility can fully account for the activity.

The role of the RCZ: processing subjective difficulty

In the ROI analysis for the RCZ we found main effects for both subjective difficulty and for prime-response compatibility, the latter replicating the main finding from our previous study (Teuchies et al., 2016) that the RCZ showed increased activation on incompatible trials (when subliminal, conflicting information was present). The current study and our previous study thus show that the RCZ and the anterior insula are sensitive to subliminal conflict, but the main effect for subjective difficulty observed in the current study suggests that, at least in the context of the response priming task in this study, activity in the RCZ reflects the processing of the subjective difficulty of the task. For the RCZ, this might have some implications for its function with regard to conflict monitoring for instance. The RCZ is part of the anterior cingulate cortex (ACC) which has often been linked to conflict monitoring and response competition (Kiehl et al., 2000; van Veen et al., 2001; Botvinick et al., 1999; 2001; Barch et al., 2000; Cohen et al., 2000; MacDonald et al., 2000; Carter et al., 1998; 2000; Van Veen & Carter, 2002). It has been recently suggested that activity in the RCZ reflects task difficulty rather than conflict between different response alternatives (Wisniewsky et al., 2016) which the results of the current study support. Activity in the RCZ increased with increasing subjective difficulty, independent of prime-response compatibility and controlled for reaction times, suggesting that rather than being involved in mere conflict monitoring, the RCZ is also involved in processing the subjective difficulty of the task. Of course, conflict and task difficulty are related as conflicting trials are reported by the participants to be more difficult to respond to as evidenced by the behavioral data of the current study as well as by previous studies (Desender et al., 2014; 2016). The coordinates of the RCZ region found by Teuchies et al. (2016) [MNI 6 20 43] and in the current study [MNI 0 17 52] lie in close proximity to coordinates of the RCZ reported by Kiehl et al. (2000) [MNI 4 22 40] to be more active when an inappropriate response on a go/no-go task was activated. According to Kiehl et al. (2000) this activation in the RCZ is part of the cognitive division of the ACC which is thought to be involved in detecting response conflict (Devinsky, Morrell, & Vogt, 1995). Carter et al. (1998) also reported similar coordinates [tailarach 4 25 43 / MNI 4 23 47] and suggested that the RCZ is involved in the detection of conditions under which errors are more likely to occur rather than being involved in detecting actual errors themselves. This latter claim by Carter et al. (1998) would match our interpretation of the current results that the RCZ also processes the difficulty of the response, as conditions under which errors are more likely to occur would be more difficult than conditions that do not lead to more errors. To summarize, despite the large body of evidence that links the RCZ to conflict monitoring, we think it might be possible that the RCZ is also involved in processing the subjective difficulty of the task, rather than conflict per se.

The role of the anterior insula in metacognition

We found that activity in the anterior insula increased together with the sense of subjective difficulty, again independent from prime-response compatibility and controlled for reaction times. As in the RCZ, in the anterior insula we also found higher activation due to the presence of subliminal conflict. This implies that it is not the mere presence of conflict that drives the activation in the anterior insula, but rather the difficulty of the task. A possible explanation for these results might be the involvement of the anterior insula in interoceptive awareness (Craig, 2009; Grupe & Nitschke, 2013; Gu, Hof, Friston, & Fan, 2013), combined with the observation that the anterior insula has also been linked to decision-making, cognitive control and performance monitoring (Thielscher & Pessoa, 2007; Cole & Schneider, 2007; Dosenbach et al., 2007; Craig, 2009). Interoception can be described as the sense of the physiological condition of the body, or the perception of sensory events occurring within one's body (Craig, 2002; 2003; Grupe & Nitschke, 2013). In the current study, sensing subjective difficulty could be seen as a form of interoceptive awareness as well. The current results imply an important role for the anterior insula in metacognition via its role in interoceptive awareness, as it is likely that interoceptive awareness led participants to differentiate between easy and difficult responses. This explanation is also supported by the finding that in the current study neither reaction times, nor prime-response compatibility can account for the brain activity correlated with subjective difficulty, which leaves room for interoceptive awareness as a source of information to base the subjective difficulty ratings on.

The RCZ and the anterior insula co-activated

The anterior insula and the ACC are strongly connected and are thought to be working together as complementary limbic sensory and motor regions (Cole & Schneider, 2007; Dosenbach et al., 2007; Craig, 2009; Gu et al., 2013). Because of this strong functional connection between the RCZ and the anterior insula we carried out a mediation analysis in which we wanted to see how well we could explain the subjective rating using activity from both the anterior insula and the RCZ. We found that the subjective ratings were best explained by the RCZ via the anterior insula. This implies that the signal would first pass through the RCZ, which might then be triggered to engage more effort, the physiological signals of which might then be perceived through interoceptive awareness by the anterior insula which in turn would lead to the subjective ratings. It has been shown that response-conflict leads to motor hesitation (Questienne, Atas, Burle, & Gevers) and effort-related sympathetic activity such as cardiac deceleration (Kuipers et al., in press). Combined with the observation that participants can indeed reflect on their experience of increased mental effort (Naccache et al., 2005), it seems plausible that participants could sense the increased effort engaged by the RCZ and other conflict related physiological changes through interoceptive awareness, which would be reflected by increased activity in the anterior insula. This relationship between the RCZ and the anterior insula would also be expected based on previous studies, in which the presence of conflicting information and subsequent ACC activity is linked to event-related components (ERPs) such as the N2 (Van Veen & Carter, 2002; Ullsperger, Fischer, Nigbur, & Endrass, 2014; Jiang, Zhang, & van Gaal, 2015; Desender et al., 2016) and the P3 (Coles, Gratton, Bashore, Eriksen, & Donchin, 1985; Purmann, Badde, Luna-Rodriguez, & Wendt, 2011; Desender et al., 2016). These components are typically found between 200 – 300 ms (N2) and 300 – 400 ms (P3) after stimulus onset, meaning they occur very fast after a response is made. This fast timing is the reason we had expected the RCZ to be the first to respond to increased difficulty during action-selection, followed by the anterior insula which would then lead to a metacognitive judgement. Of course it has to be noted that based on the current data it is difficult to make any claims about the direction of the signal since the temporal resolution of fMRI does not allow us to determine in what order the RCZ and the anterior insula were activated during a trial.

The influence of reaction times

It has been suggested that reaction times might serve as a proxy for task difficulty (Kiani, Corthell, & Shadlen, 2014). This would imply that participants base their subjective difficulty ratings on how long they thought it took them to respond. The results of the current study did not indicate that this was the case, which is similar to findings by Desender et al. (2016) who found that the effect of congruency on metacognitive experience was also present in a subset of the data that was matched for reaction times. We did not find overlapping brain activity when we looked at the effects of reaction times compared to the effects of the subjective ratings. Looking at brain activity correlated solely with reaction times when controlling for prime-response compatibility and subjective difficulty we found a small cluster of activation in the postcentral gyrus (Brodmann area 2) which would be part of the somatosensory cortex which mostly represents the fingers (see e.g. Kurth et al., 2000; McGlone, Kelly, Trulsson, Francis, Westling, & Bowtell, 2002; Nelson & Chen, 2008). While we have no clear ideas on why this area is activated when we look at the reaction times, it may be that awareness of the time it takes to respond is somehow related to proprioception. Participants may be aware that it takes longer for their fingers to move and respond to the target on certain trials. Rather than a sense of subjective difficulty which would involve the anterior insula and the RCZ, reaction times might trigger a more embodied feedback, hence activating the somatosensory cortex.

Conclusion

Overall it seems that the subjective sense of difficulty is most strongly represented in the RCZ and the anterior insula, two regions that are functionally closely connected. We found that activity in these regions increased when subjective difficulty increased independent of prime-response compatibility and controlled for reaction times. Despite the RCZ already being linked so often to conflict detection, the results of the current study suggest it also processes subjective task difficulty. In the context of the response priming task used in the current study, the RCZ could be engaged to invest goal-directed effort and activity in the anterior insula could reflect interoceptive awareness to pick up signals that participants could base their judgement of subjective difficulty on. Since the RCZ and the anterior insula appear to be so tightly linked and are almost always activated in unison, future research is needed to look further into their unique contributions to conflict detection, sense of subjective difficulty and metacognition in general.

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General Discussion

In the present thesis, I set out to look into the processes involved in making free choices, because a clear understanding of this quintessential human behavior is still lacking. I was especially interested in the imfluence of bottom-up and top-down processes on making free choices and how they interact. Based on previous studies a subliminal response priming paradigm was chosen to manipulate choices throughout the various experiments that were carried out for this thesis because this paradigm has been tried and tested in the field and yields robust priming effects (Vorberg, Mattler, Heinecke, schmidt, & Schwarzbach, 2003; Schlaghecken & Eimer, 2004; Wenke, Fleming, & Haggard, 2010; Sidarus et al., 2013; Furstenberg, Breska, Sompolinsky, & Deouell, 2015). We collected imaging data of participants carrying out the response priming task which were analyzed using both univariate analysis methods and multi-voxel-pattern analysis (MVPA) to look at the neural correlates of making free choices. The response priming paradigm was also combined with a top-down manipulation to study its modulating effect on free choices. In this section I will elaborate on the results that were reported in the empirical chapters of this thesis. First, I will start by giving a brief overview of the most important findings.

Summary of empirical results

In **chapter 1**, we wanted to study bottom-up influences on free choices so we used fMRI to collect imaging data of participants carrying out the response priming task in order to investigate which brain regions were involved in making free choices and how activity in these regions was affected by the subliminal primes. We also aimed to look specifically at the rostral cingulate zone (RCZ) as there is an ongoing debate about its exact role and function regarding the voluntary decision making process. We found that making free choices was related to activity in the RCZ, the anterior insula, the dorsolateral prefrontal cortex (DLPFC) and the pre-supplementary motor area (pre-SMA). These brain regions are part of a 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) and the results of the study reported in chapter 1 showed that activity in some regions of this voluntary action network could be modulated by subliminal information, especially the RCZ and the anterior insula. Based on the findings of this study we proposed that the RCZ and the anterior insula were both involved in overcoming conflict between different response alternatives when making free choices. However, results from the studies reported in chapters 2 and 4 showed that this interpretation might be inaccurate, as will be explained later when discussing the results of these chapters. Furthermore, we suggested that the DLPFC and the pre-SMA were responsible for implementing and carrying out the chosen response after conflicts had been resolved. In **Chapter 2**, we reanalyzed the data from chapter 1 using MVPA to look into an open issue related to the studies of Soon et al. (2008; 2013) who used MVPA to investigate to what extent free choices were determined by preconscious processes. Soon et al. (2008; 2013) found that it was possible to decode unconscious intentions from brain activity that preceded awareness of these choices. However, an alternative interpretation of these results suggested that it was not an unconscious intention that was decoded but rather an unconscious bias in the system that influenced free choice (Bode et al. 2014). The main aim of this chapter was to investigate how unconscious biases affected the decoding of response alternatives from brain activity. We found that decoding accuracy in the precuneus was influenced by unconscious biases indicating that the decoding of intentional choices was susceptible to unconscious biases in the system. The results of the study reported in chapter 2 suggested that the precuneus might accumulate information and integrate external and internal signals leading to a response. Additionally, we investigated whether we could decode choices from the RCZ and the anterior insula, two regions that we thought might be important for making free choices based on previous research (see e.g. Brass & Haggard, 2008; 2010) and based on the results from the univariate analyses reported in chapter 1. We did not find evidence that these regions contained information about the choices participants made. This finding questioned the role of the RCZ and the anterior insula in coding intentional choices and suggested that RCZ activation in univariate analyses might reflect general differences between conditions such as effort or difficulty, a topic we addressed in chapter 4. In **Chapter 3**, we combined the response priming paradigm with an anti-free-will-belief manipulation (Vohs & Schooler, 2008; Rigoni, Kuhn, Sartori, & Brass, 2011) to investigate how top-down processes modulated the influence of subliminal bottom-up information. We observed a significant decrease in free-will belief in the anti-free-will group. This group also showed an increased susceptibility to subliminal primes compared to the control group. This effect was only visible for free choices, not for cued choices, suggesting that cued choices were less susceptible to the manipulation. Possible explanations for these findings were a reduction of intentional involvement while making free choices and a weaker task set activation due to the manipulation. These results suggested that reducing conscious top-down involvement in making free choices left more room for unconscious influences to guide and influence these choices. These findings offer further support for the idea that subliminal influences on our behavior are not fully automatic or uncontrollable, but can indeed be influenced by conscious high-level beliefs. In **Chapter 4**, we wanted to look at the neural correlates of metacognition in the context of response priming by investigating a particular type of metacognitive process, namely the subjective experience of fluency in action-selection (See also Desender, Van Opstal, & Van den Bussche, 2014; Desender, Van Opstal, Hughes, & Van den Bussche, 2016). Contrary to the previous chapters, to manipulate fluency in action-selection we used a subliminal response priming paradigm that only consisted of cued choices. Participants then had to engage in the metacognitive process of rating how difficult they felt it was to respond fast and accurately to the target stimuli. Participants rated incompatible trials during which subliminal primes were interfering with the correct response as more difficult than trials on which primes facilitated the correct response. This increased sense of subjective difficulty was mirrored by the correlation between the subjective ratings and activity in the RCZ and the anterior insula, independent of prime-response compatibility and controlled for the influence of reaction times. To return to the findings of chapter 1, despite the RCZ being linked closely to conflict detection (see e.g. Botvinick, Braver, Barch, Carter, & Cohen, 2001), the results of the study reported in chapter 4 suggested that the RCZ might be processing subjective task difficulty rather than conflict.

The role of the RCZ in making free choices

Ongoing debate

The role of the RCZ in voluntary behavior is still a topic of ongoing debate. One of the aims of this thesis was to further investigate the role of the RCZ in making free choices. Previous studies using free choice paradigms have consistently found the RCZ to play a role in making free choices (Lau, Rogers, Ramnani, & Passingham, 2004; Walton, Devlin, & Rushworth, 2004; Forstmann, Brass, Koch, & von Cramon, 2006; Mueller, Brass, Waszak, Prinz, 2007; Demanet, De Baene, Arrington, & Brass, 2013; Orr & Banich, 2014). Until now, the role attributed to the RCZ was to choose between different response alternatives (Forstmann et al., 2006; Demanet et al., 2013; Brass & Haggard, 2008; Cunnington, Windischberger, Robinson, & Moser, 2006; De Baene, Albers, & Brass, 2012; Lau et al., 2004; Mueller et al., 2007; van Eimeren et al., 2006; Venkatraman, Rosati, Taren, & Huettel, 2009; Walton et al., 2004). However, activity in the RCZ has also been linked to conflict monitoring and conflict resolution rather than intentional processes (Botvinick et al, 2001; Nachev, Rees, Parton, Kennard, & Husain, 2005). Because of these different findings regarding the RCZ, there is an ongoing debate about whether the RCZ truly processes the choice between different response alternatives or whether activity in the RCZ simply reflects differences in effort or task difficulty between experimental conditions (Wisniewski, Goschke, & Haynes, 2016). Based on the findings from previous studies it is apparent that the function of the RCZ has not yet been sufficiently clarified.

Imaging findings of the present thesis

In the study reported in Chapter 1, we observed activity in the RCZ when we contrasted free-choices with cued-choices, thus replicating the findings of previous studies (Forstmann et al., 2006; Demanet et al., 2013; Orr & Banich, 2014). In the region of interest analysis, we found that activity in the RCZ was higher for incompatible trials compared to compatible trials or neutral trials. This pattern was found independent of choice type, so for both cued choices and free choices. This activation pattern also mirrored the behavioral data in which the incompatible condition of both cued-choice trials and free-choice trials showed higher reaction times and error rates compared to compatible trials and neutral trials. Based on these results we concluded that the RCZ was sensitive to conflict, even if the cause of this conflict and possibly even the conflict itself were subliminal. These findings suggest that the RCZ is most likely not the brain region that chooses voluntary responses since the observed pattern of activity was similar for both cued-choice trials and free-choice trials, and participants never really made a choice in the cued-choice condition, instead they followed external cues. The results of chapter 2 offered further indications that the RCZ was not involved in choosing which response to execute. One of the aims of chapter 2 was to see whether we could use MVPA to decode the choices people made from brain activity in the RCZ. The results of chapter 2 showed that we were unable to do so, which is in line with another study that was unable to decode voluntary intentions from the RCZ (Wisniewsky et al., 2016). A possible explanation mentioned by the authors was that previous studies which were able to decode intentions from the RCZ (see e.g. Wisniewski, Reverberi, Tusche, & Haynes, 2015) did not sufficiently control for task-difficulty (Todd, Nystrom, & Cohen, 2013) implying that it may have been difficulty that was decoded in these studies rather than intentions. The idea that the RCZ processes difficulty rather than intentions or conflict is further supported by the results of chapter 4. In this chapter, we looked at the neural correlates of the experience of fluency of action-selection in the subliminal response priming task. Participants had to indicate on every trial how hard it was for them to respond as fast and as accurately as possible to the target arrows. The imaging results of this study showed that activity in the RZC increased together with subjective difficulty, independent of prime-response compatibility and reaction times. This indicates that activity in the RCZ indeed reflected subjective difficulty rather than choosing between response alternatives or monitoring conflict. This interpretation is compatible with the results of a recent study considering the role of the RCZ in decision making in which it was found that activity in this region stayed low until the end of the trial, at which point a single response had already been chosen (Neta, Nelson, & Petersen, 2016). This would be incompatible with the idea of the RCZ being involved in action selection or intention processing, as this would have required the RCZ to come online earlier during the trial. Neta et al. (2016) argued that the RCZ was involved in reporting performance signals such as errors and conflict/ambiguity at the end of the trial. This view is compatible with the results of the current thesis as reporting or monitoring the difficulty of a response is something that would take place near or at the end of the trial when a response has already been selected and executed. To summarize, the results of the studies carried out in the current thesis suggest that activity in the RCZ does not reflect monitoring and/or resolving conflict and choosing between different response alternatives, but rather reflects processing the subjective difficulty of the task.

Functional Connectivity with the Anterior Insula

A region that has often been found to be co-activated with the RCZ is the anterior insula (Cole & Schneider, 2007; Dosenbach et al., 2007; Craig, 2009; Brass & Haggard, 2010; Gu, Friston, & Fan, 2013). In chapter 1, the anterior insula showed the same activation pattern as the RCZ. For incompatible trials we observed increased activity compared to compatible trials and neutral trials, across both cued choices and free choices. This indicated that both cued choices and free choices were sensitivity to subliminal conflict in a similar way and in light of the previous discussion about the RCZ, this might indicate that the anterior insula is also involved in processing subjective difficulty. This interpretation was supported by the results from the study reported in chapter 4. In this study the anterior insula showed increased activity in relation to increased subjective difficulty, also (as in the RCZ) independent of prime-response compatibility and reaction times. Unfortunately, based on the data collected in the current thesis it is not possible to further differentiate between the different functions of the anterior insula and the RCZ. Considering the role the anterior insula has in interoception (Craig, 2009) we argued in chapter 4 that the anterior insula might be responsible for the perception of interoceptive signals. This matches the idea proposed by Brass and Haggard (2010), that the anterior insula might signal the affective consequences of voluntary decisions and monitors whether a chosen action was successful or not. Based on the results of chapter 4 this monitoring role might also include keeping track of how difficult it felt to choose a response. This interpretation, however, is speculative and needs further study to confirm or reject it.

Making choices

Based on the findings of chapter 1 we initially thought that the RCZ and anterior insula were involved in processing conflicting response alternatives and in choosing the option that has to be executed. As mentioned earlier in this discussion, the results of chapter 2 and 4, however, indicated it was unlikely that the RCZ and the anterior insula were involved in processing conflicting response alternatives and in choosing one over the other, but rather were involved in processing more general aspects of the decision process such as subjective difficulty. If the choices are not made in the RCZ or the anterior insula, then where are they made? Results from studies by Soon et al. (2008; 2013) and from the study reported in chapter 2 point to the precuneus as a possible region where the actual choice between several response options could be made. Soon et al. (2008; 2013) found that they could decode voluntary action intentions from the precuneus and the frontopolar cortex. In chapter 2 we used MVPA to decode choices from brain activity and we also found that we could do this from a region overlapping with the precuneus region reported by Soon et al. (2008). We were not able to decode choices from activity patterns in the frontopolar cortex. According to Soon et al. (2008) the frontopolar cortex was the first cortical stage at which the decision making process started to take place. The precuneus on the other hand was thought to be involved in the storage of the decision until it reached awareness. This means that in the precuneus the information regarding the decision would be available almost until the point where the decision was actually carried out. In the frontopolar cortex, on the other hand, the information about a choice would already be available some time before the decision was carried out. Considering the fact that in the study reported in chapter 2 we were decoding decisions at the time of the response, it is possible that by that point in time the information was no longer available in the frontopolar cortex, but was still there in the precuneus. In the region of interest analysis for the precuneus we looked at the prediction accuracy per condition and found an interaction between choice type (free, cued) and prime-response compatibility (compatible, incompatible, neutral). We were best able to decode choices from the free choice incompatible condition and from the cued choice compatible and neutral conditions. Our explanation for this counterintuitive pattern of results was that in these three conditions the intention to act was highest due to the input from different bottom-up and top-down sources of information that accumulated into the final choice. In the cued-choice compatible and neutral conditions the external, bottom-up input from the primes and the targets led to the strongest intentional signal. Arguably, in the free choice incompatible condition top-down internal effort was needed to overcome the incompatible prime, thus leading to a strong intentional signal. Based on this assumption it seemed plausible that one of the roles of the precuneus would have been the accumulation and integration of evidence from different sources for one or the other response alternative until enough evidence was accumulated to cross a threshold and a choice was made. This decision process is similar to the decision process explained by the diffusion model (Ratcliff, 1978; Ratcliff & McKoon, 2008; Smith & Ratcliff, 2004, 2009). This model assumes that a choice is made when enough evidence for that choice reaches a certain decision threshold. According to Ratcliff and McKoon (2008) one of the assumptions of the diffusion model is that decisions are made by a noisy process that accumulates information over time from a starting point toward one of two response criteria or boundaries (Figure 1). The starting point is ‘z’ and the boundaries are ‘a’ (“response A”, left hand for instance) and ‘0’ (“response B”, right hand for instance). A choice is made whenever enough evidence is accumulated to reach one of the boundaries. The accumulation rate of information is called the drift rate (v). This rate is determined by the quality of the information that comes from the stimulus or other sources that influence the choice. In a typical experiment, the drift rate would vary

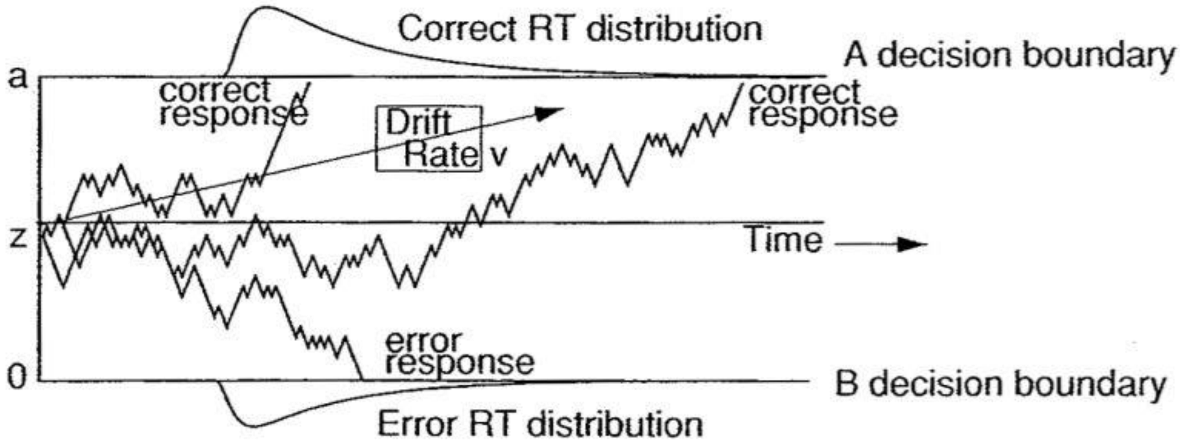

Figure 1. The diffusion decision model. Three simulated paths with drift rate v, boundary separation ‘a’ and ‘0’, and starting point z. Adapted from Ratcliff and McKoon (2008).

for each stimulus condition, because different stimulus conditions would differ in difficulty. In case of a response priming experiment the drift rate could represent the match between a prime and the target. A compatible trial where the prime and the target are cueing the same response would lead to a higher drift rate and thus a faster response than an incompatible trial. For free choices the evidence for a choice cannot come from the target, but it can come from the prime and other sources such as action intentions of the participant. Again, if the intentions match the prime, this will lead to a higher drift rate and a faster choice. This also matches behavioral findings from studies looking into subliminal priming (e.g. Forstmann et al., 2010; Mattler & Palmer, 2012; Vorberg et al., 2003; Wenke et al., 2010; Sidarus et al., 2013; Furstenberg et al., 2015). There are some constraints however, to the extent that these models can be applied, such that diffusion models for simple two-choice decisions should only be applied to choices that are made relatively fast (mean RTs less than about 1000 to 1500 ms) and only to choices that involve a single-stage decision process (Ratcliff & McKoon, 2008). Response priming is a task with parameters that fall within these constraints, with simple choices and mean RTs usually below 500 ms., which means that diffusion models could account for our findings and that the proposed mechanism by which the precuneus might be involved in choosing responses is at least plausible. In summary, our interpretation of the role of the precuneus matches that of Soon et al. (2008), but beyond storing or maintaining the decision, the precuneus would also be involved in accumulating evidence for the decision.

Top-down influences on voluntary choices

Another aim of the current thesis was to look at the interaction between bottom-up and top-down factors while making free-choices. To investigate how this interaction might work, in chapter 3 we combined the response priming paradigm with a free-will-belief manipulation (see e.g. Vohs & Schooler, 2008; Rigoni et al, 2011). We hypothesized that by reducing belief in free-will we would reduce participants' intentional involvement in the choices they were making. This reduced intentional involvement should then have resulted in a larger influence from the subliminal primes, as participants would have been less willing to choose their own responses, instead relying more on the available external information to guide their choices. One possibility was that the manipulation would have affected both cued-choice and free-choice trials to the same degree. However, we also thought that it was possible that the manipulation would only affect the free-choice trials because in this condition responses were self-determined and could thus have been more sensitive to a manipulation of free-will belief. The results of Chapter 3 confirmed the latter hypothesis and showed that only the free-choice condition was affected by the anti-free-will belief manipulation. Participants in the anti-free-will belief group responded faster in the compatible free-choice condition compared to participants in the control group. This shows that the primes triggered a facilitation process in the free-choice compatible condition of the anti-free-will group, since their responses were significantly faster than the neutral primes in this condition, which was not the case in the control group. Contrary to our expectations we did not observe a change in the interference effect in the anti-free-will group compared to the control group. Exactly why this is the case is not clear. A possible explanation could be that the slight increase in time between the prime and the response in the free-choice condition affected the facilitation of a response by a compatible prime more than the interference by an incompatible one. Looking at the data of Schlaghecken and Eimer (2000) it appears that a slight increase of the timing between the prime and the target leads to a steeper increase in reaction times on compatible trials compared to the decrease in reaction times on incompatible trials, meaning that it takes more time for the interference effect to be significantly reduced. This might explain why we observed a reliable difference between the groups on the facilitation effect but not on the interference effect. Of course, this is also speculation and further research is needed to see whether this is indeed the case. The larger facilitation effect in the anti-free-will group indicated that the belief manipulation made the processing of the unconscious information easier. According to Kiefer (2007), the influence of top-down processes happens via previous reactions, current intentions, attention to the stimuli, or instructions that activate a certain task-set. Based on the results reported in chapter 3 it seems that the anti-free-will-belief manipulation mainly influenced the intentions of the participants and probably also the task-set in the free-choice condition. The findings of the study reported in chapter 3 indicated that participants in the anti-free-will group were less intent on choosing freely, and thus were led more by the subliminal information on free choices, whereas people in the control group were intent more on choosing freely and were therefore less prone to follow the primes. Contrary to the free-choice condition, only a minimum of intentional involvement was needed to respond correctly in the cued-choice condition. Participants could simply follow the target arrows without having to intentionally make up their minds with regard to which response they wanted to choose. Similarly, the manipulation might also have affected the task-set, but only for the free-choice trials as responses to the cued-choice trials by participants in the anti-free-will belief group were not different from the control group. Participants in the anti-free-will belief group, however, still responded slower on free-choice trials compared to cued-choice trials, suggesting that some voluntary response processes were still operating and that the manipulation did not deprive them completely of their intention to respond freely, but might have weakened the activation of the task-set sufficiently to reduce the importance of responding freely on free-choice trials. As Kiefer (2007) pointed out, next to intentions, attention is also a crucial top-down process and even a prerequisite for the priming effects to exist, because without allocating at least some minimal amount of attention to the primes it becomes impossible for them to influence our behavior. The fact that our design used a mix of cued-choice and free-choice trials might account for the fact that participants in the anti-free-will belief group kept paying attention to the primes. As shown by the similar reaction times in the cued-choice conditions between the anti-free-will group and the control group, we assumed that participants still wanted to respond fast and accurately to the targets in the cued-choice condition, thereby still investing attention into the task. This means that they also processed the primes on the free-choice trials because they could never know if a trial was going to be free or cued before the target appeared. Interestingly, the results of chapter 3 ran somewhat counter to what one could have expected based on previous studies in which attentional allocation was also similar across conditions, but reduced priming effects were found instead of increased priming effects (e.g. Eimer & Schlaghecken, 1998; Schlaghecken & Eimer, 2001). For instance, when mixing target arrows with letter targets “L” and “R” to cue left or right responses, reduced priming effects were observed (Eimer & Schlaghecken, 1998). Based on these previous findings Schlaghecken and Eimer (2004) concluded that only stimuli that were part of the currently active task-set could influence behavior, possibly because the action-intentions changed with the stimuli. In the study reported in chapter 3 of the current thesis, however, the stimuli did not change between conditions and we found increased priming effects instead of reduced priming effects. This shows that even if the stimuli are still part of the currently activated task-set, intentions can be manipulated and reduced top-down and modulate the processing of the primes. Moreover, the results of the study reported in chapter 3 showed that just looking at the location where subliminal primes will appear, is sufficient for them to influence behavior, even if the intentional involvement and the task-set activation are reduced.

Metacognition and response priming

In chapter 4 we looked at the subjective experience of subliminal response conflict and more specifically the neural correlates of this experience. An open question that remained was whether conflict detection and the metacognitive experience of conflict had dissociable neural correlates. In the study reported in chapter 4 we looked at fluency of action-selection which we manipulated using subliminal response priming. We asked participants on a trial-by-trial basis how hard it was for them to respond as fast and as accurate as possible, thereby obtaining metacognitive measures about the subjective difficulty of the responses. In this experiment only cued-choices were used, as during pilot experiments we found no reliable differences in subjective difficulty ratings between the free-choice conditions and responses were always rated as more difficult in the free-choice condition compared to the cued-choice condition. It is possible that due to the lack of a target-prime combination in the free-choice condition (as is present in the cued-choice condition) it is harder for participants to sense the conflict that is induced by the combination of an incompatible prime-response pair.

Based on the results of the study reported in chapter 4 it is seems plausible that the subjective sense of difficulty and conflict detection are linked. When we correlated the subjective difficulty ratings with neural activity to see which brain regions correlated with this metacognitive experience we found the anterior insula and the RCZ to be activated more for responses that were rated as more difficult. Although this activation was independent of prime-response compatibility, in the ROI analysis these regions also showed a main effect for prime-response compatibility, such that activity was higher for incompatible trials, indicating that the same regions that process conflict are also processing the subjective difficulty of the response. This could mean that participants used the sense of conflict to judge the difficulty of the response, but it could also mean that these regions merely processed difficulty of the response and that they also showed a main effect for prime-response compatibility because conflicting trials happen to be more difficult in general. Based on the results it remains an open question whether conflict detection and the metacognitive experience of conflict have dissociable neural correlates.

Conclusion

One of the aims of this thesis was to look into the interaction of unconscious bottom-up influences and more conscious top-down influcences while making free choices. Based on previous studies and results obtained throughout the thesis the RCZ was used as a proxy for the neural correlates of the intentional control of behavior. The results indicate that the RCZ does not exclusively process voluntary behavior and that the RCZ is also not involved in choosing between different response options, as had thus far been assumed. Based on the results of this thesis it seems most likely that the RCZ, together with the anterior insula, processes the subjective difficulty of the response, rather than the content of the response itself. Based on the results of chapter 2 the choice itself might be made in the precuneus. It seems plausible that the precuneus is involved in accumulating bottom-up and top-down information from different sources until a decision threshold for on or the other response option is reached. With regard to top-down influences, the results of the current thesis show that manipulating top-down processes can indeed influence how subliminal bottom-up information is processed, even in the context of free choices. A reduction of the intentional involvement in making free choices can make people more susceptible to bottom-up information and so increase its impact on behavior.

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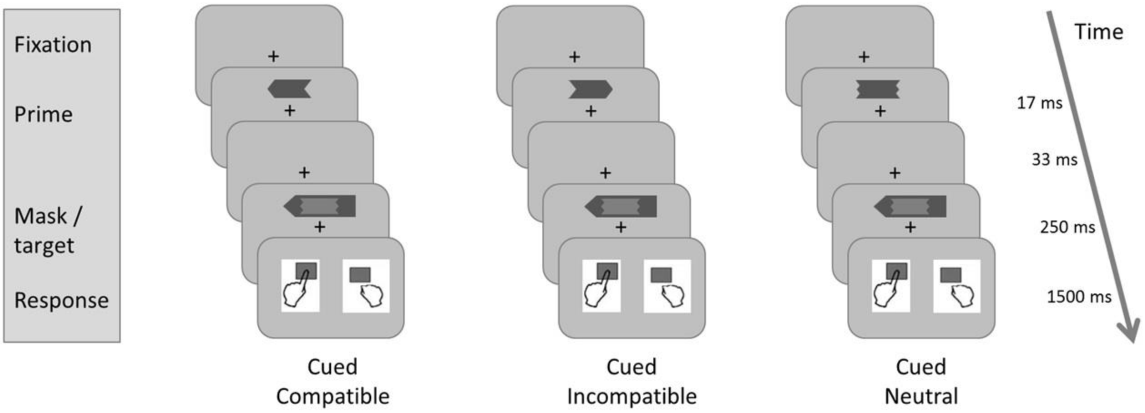
Nederlandse Samenvatting

De vraag hoe mensen vrije keuzes kunnen maken uit verschillende alternatieven fascineert wetenschappers al sinds het onstaan van de psychologie als wetenschapstak (James, 1892). Ondanks het gegeven dat we elke dag een enorme hoeveelheid keuzes maken en dit daarom een zeer relevant onderwerp is, weten we eigenlijk nog relatief weining over deze fundamentele menselijke eigenschap, in het bijzonder over de interactie tussen zogenaamde bottom-up en top-down processen die beiden een aantoonbare invloed hebben op het vrije keuzeproces. Maar wat zijn vrije keuzes eigenlijk precies? Volgens Bode et al. (2014) zou je intuitief zeggen dat vrije keuzes de onafhankelijkheid vereisen van externe factoren, of zelfs van hersenprocessen. Om deze reden vermijden veel auteurs de termen “vrije wil” of “vrije keuze”, maar spreken ze liever over termen zoals “vrijwillige keuzes” of “interne beslissingen”. Haggard (2008) definieert vrijwillige acties door ze te contrasteren met stimulus-gedreven acties. Idealiter zijn vrijwillige acties maximaal onafhankeijk van externe stimuli en liggen ze aan het uiteinde van een spectrum met eenvoudige reflexen aan de andere kant. Anderen maken het verschil tussen vrijwillig en stimulus-gedreven door te refereren aan “actieve” vrije keuzes en “passieve” eenvoudige neigingen of verlangens (Batthyany, 2009). Jammer genoeg ontbreekt het aan een duidelijke definitie van wat vrije keuzes precies zijn. Wanneer ik doorheen deze thesis refereer aan “vrije keuzes” bedoel ik daarmee dat het responsen zijn die door de participant zelf zijn gekozen in de afwezigheid van (bewust waargenomen) externe cues waarop ze hun respons zouden kunnen baseren en die tegenovergesteld zijn aan “gecuede keuzes” waar de respons duidelijk wordt aangegeven door een externe stimulus. Binnen de psychologie hebben voornamelijk twee onderzoeksvelden naar het maken van vrije keuzes gekeken, namelijk cognitieve neurowetenschappen (zie bijv. Brass & Haggard, 2008; Demanet, De Baene, Arrington, & Brass, 2013; Brass, Lynn, Demanet, & Rigoni, 2013; Orr & Banich, 2014) en sociale psychologie (zie bijv. Baumeister, Bratslavsky, Muraven, & Tice, 1998; Holland, Hendriks, & Aarts, 2005; Dijksterhuis, Bos, Nordgren, & van Baaren, 2006; Vohs & Schooler, 2008). Recent onderzoek binnen de cognitieve neurowetenschappen suggereert dat vrije keuzes worden beïnvloedt door zowel bottom-up als top-down factoren (Demanet et al., 2013). Bottom-up verwijst naar informatie (bijv. externe cues) die onbewust kan worden waargenomen en die een invloed heeft op vrije keuzes zonder dat we daar over moeten nadenken. Top-down verwijst naar meer bewuste processes zoals aandacht, intenties of een bepaalde taak-instructie die actief is tijdens het experiment (Kiefer, 2007). Er wordt gesuggereerd dat bottom-up en top-down invloeden van elkaar kunnen worden onderscheiden op hersenniveau (Demanet et al., 2013). In hun studie vonden Demanet et al. (2013) dat het *default mode network* (Raichle et al., 2001) actief was tijdens keuzes die door bottom-up factoren werden beïnvloed. Voor keuzes die werden beïnvloed door top-down factoren was de rostral cingulate zone (RCZ) actief, een hersengebied dat deel uitmaakt van het intentionele actie netwerk (Brass & Haggard, 2008). Naast de cognitieve neurowetenschappen heeft ook de sociale psychologie interesse in hoe bottom-up en top-down factoren een invloed hebben op vrije keuzes. Ook al hebben we het gevoel dat onze keuzes het resultaat zijn van bewuste processen en beslissingen, recent sociaal psychologisch onderzoek heeft uitgewezen dat vrije keuzes sterk afhankelijk zijn van onbewuste processen en dat doelen onbewust kunnen worden geactiveerd en nagestreefd (Custers & Aarts, 2010). Middels priming van sociale concepten bijvoorbeeld, is onderzocht hoe bottom-up informatie gedrag onbewust beïnvloedt. Holland et al. (2005) vonden dat mensen die werden blootgesteld aan de geur van allesreiniger sneller waren in het identificeren van schoonmaak gerelateerde woorden en zelfs ook meer schoonmaak gerelateerd gedrag lieten zien. Recent onderzoek binnen de sociale psychologie heeft ook gekeken naar hoe het onbewust verwerken van informatie keuzeprocessen beïnvloedt. In een studie van Dijksterhuis en collega's (2006) werd participanten verhinderd om na te denken over complexe problemen door ze tegelijkertijd een tweede taak te laten uitvoeren. Het resultaat was dat keuzes die gemaakt waren zonder er over na te denken als beter werden ervaren. Dit toont aan dat onze doelen en het gedrag om die doelen te bereiken, kunnen worden beïnvloed door onbewuste informatiebronnen (Custers & Aarts, 2010). Een manier waarop sociale psychologie naar de invloed van top-down factoren heeft gekeken, is door het gebruik van een anti-vrije-wil-geloof manipulatie (zie bijv. Baumeister et al., 2009; Rigoni, Kuhn, Sartori, & Brass, 2011). Het is aangetoond dat het lezen van een tekst waarin staat dat vrije wil een illusie is een invloed heeft op de motorische voorbereiding van een handeling, zoals blijkt uit een verminderd bereidheids potentiaal (Rigoni et al., 2011).

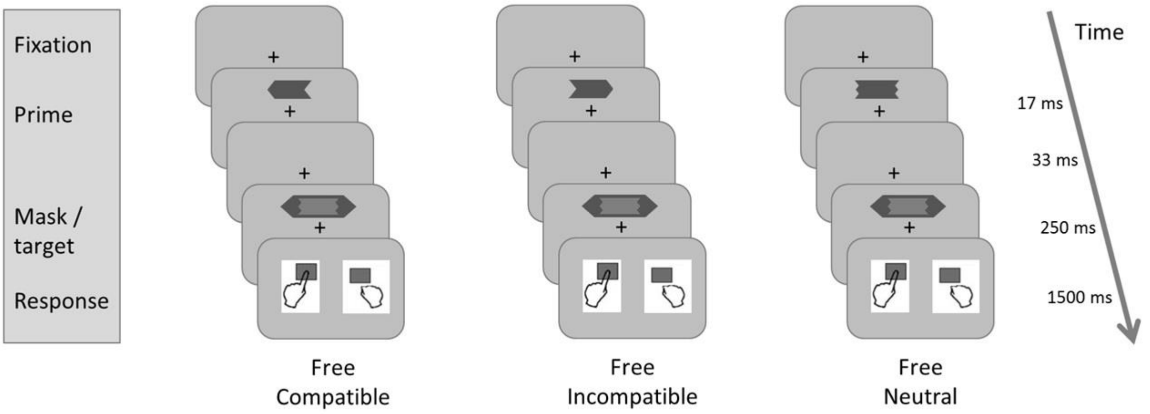
Response priming en bottom-up invloeden

Om te onderzoeken hoe bottom-up factoren ons gedrag beïnvloeden, hebben vorige studies een subliminaal respons priming paradigma gebruikt (zie bijv. Vorberg, Mattler, Heinecke, schmidt, & Schwarzbach, 2003; Sidarus, Chambon, & Haggard, 2013). In dit experimentele paradigma worden primes subliminaal gepresenteerd die vervolgens worden gemaskeerd door de target stimulus die tevens functioneert als een meta-contrast masker. Gemaskeerde priming paradigma's worden al decennia lang gebruikt om de impact van subliminale stimuli op gedrag te bestuderen (Van den Bussche, Noortgate, & Reynvoet, 2009). Reeds begin jaren '80 van de vorige eeuw werd door Marcel (1983) vastgesteld dat woorden sneller werden verwerkt wanneer ze vooraf werden gegaan door semantisch gerelateerde woorden (bijv. fiets – auto) die subliminaal werden gepresenteerd door de presentatie tijd zeer kort te houden en door de woorden te maskeren onmiddelijk na de presentatie. In een typisch response priming experiment (Figuur 1) zijn de responsen altijd extern gecued, dat wil zeggen dat participanten met de linker of de rechter hand moeten reageren op links of rechts wijzende pijlen (targets) respectievelijk (zie bijv. Vorberg et al., 2003; Sidarus et al., 2013). Voor de target pijlen in beeld komen, worden eerst de prime stimuli (kleine pijltjes) subliminaal gepresenteerd gedurende slechts 16 milliseconden. Het effect hiervan is dat participanten langzamer reageren en meer fouten maken bij incompatibele trials, waarbij de richting van de prime stimulus tegengesteld is aan die van de target stimulus, bijvoorbeeld een prime pijltje dat naar rechts wijst gevolgd door een target pijl die naar links wijst (Vorberg et al., 2003; Schlaghecken & Eimer, 2004; Wenke et al., 2010; Sidarus et al., 2013; Furstenberg, Breska, Sompolinsky, & Deouell, 2015).



Figuur 1. Schematische weergave van de trial procedure en de stimuli, aangepast van Wenke et al. (2010). Hier uitgebeeld zijn drie voorbeelden van gecuede-keuze trials uit de mogelijke combinaties van prime-respons compatibiliteit (links: compatibel; midden: incompatibel; rechts: neutraal). In ieder van deze voorbeelden reageert de participant met de linker hand.

Zowel de duratie van de primes zelf als de interval tussen de prime en het masker zijn crucial om stimuli succesvol subliminaal te kunnen presenteren. De zichtbaarheid van de primes neemt toe naarmate ook de duratie van de prime presentatie en de lengte van het interval tussen de prime en het masker toenemen (Vorberg et al., 2003). Hoe korter de duur van de presentatie van de prime en het interval tussen de prime en het masker, des te groter de kans dat de prime daadwerkelijk subliminaal wordt gepresenteerd. Eerder onderzoek heeft ook gekeken naar de invloed van subliminale primes op vrije keuzes (Schlaghecken & Eimer, 2004; Furstenberg et al., 2015; Wenke et al., 2010). In deze studies werd het klassieke “gecuede-keuze” paradigma aangepast (Figuur 2) zodat participanten werd gevraagd om bij sommige trials vrij te kiezen tussen twee responsalternatieven met de restrictie dat beide alternatieven bij benadering even vaak moesten worden gekozen over de loop van het experiment. Om aan de participanten aan te geven dat een trial een vrije keuze trial was werd er een ‘neutrale’ target toegevoegd aan het experiment. Deze neutrale target was een pijl die twee kanten tegelijk uitwees (zie de mask/target in Figuur 2). Het is aangetoond dat subliminale primes hetzelfde effect hebben op vrije keuzes dan op gecuede keuzes; dat wil zeggen, bij zowel gecuede als vrije keuzes worden participanten langzamer en maken ze meer fouten wanneer de

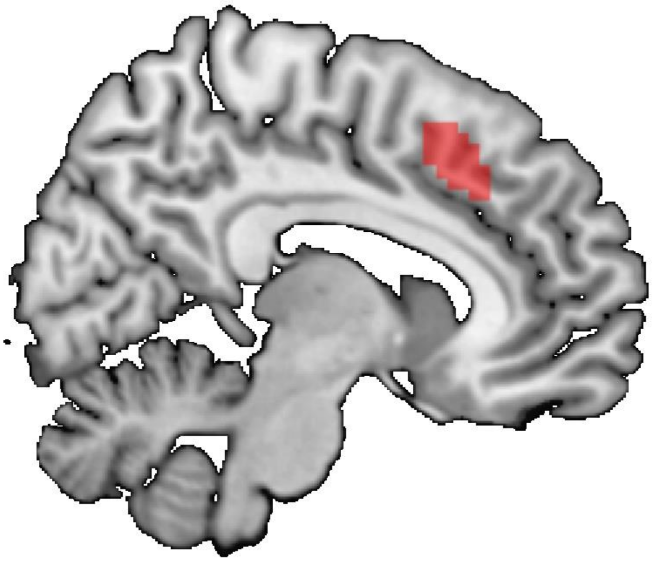


Figuur 2. Schematische weergave van de trial procedure en de stimuli, aangepast van Wenke et al. (2010). Hier uitgebeeld zijn drie voorbeelden van vrije-keuze trials uit de mogelijke combinaties van prime-respons compatibiliteit (links: compatibel; midden: incompatibel; rechts: neutraal). In ieder van deze voorbeelden reageert de participant met de linker hand.

subliminale prime incompatibel (tegengesteld) is aan de gekozen respons (Schlaghecken & Eimer, 2004; Furstenberg et al., 2015; Wenke et al., 2010). Daarnaast wordt er in de vrije keuze conditie ook een voorkeur gevonden voor de compatibele keuze. Participanten hebben de neiging om meer te reageren in dezelfde richting als de subliminale primes dan ertegenin te gaan, normaliter in zo’n 55% tot 58% van de vrije keuze trials (Wenke et al, 2010; Furstenberg et al., 2015). Interessant is ook dat Schlaghecken en Eimer (2004) hebben aangetoond dat priming effecten enkel worden gevonden bij vrije keuzes wanneer ze gemixt worden met gecuede keuzes. In experimentele blokken die uit enkel vrije keuzes bestonden, werden geen effecten van de prime gevonden. Deze observatie is consistent met de bevinding van Wenke et al. (2010). Zij gebruikten in hun experiment blokken waarin de verhouding tussen vrije en gecuede keuzes 25/75 of 75/25 was. Er werden grotere priming effecten gevonden (langzamere responsen en meer fouten bij incompatibele trials in vergelijking met compatibele trials) wanneer de verhouding vrij/gecued 25/75 was in vergelijking met 75/25. Met andere woorden, hoe groter relatief gezien het aandeel vrije keuzes is, des te kleiner de effecten van de primes op deze vrije keuzes. Om de zichtbaarheid van de primes te testen, vindt er meestal ook een prime-zichtbaarheidstest plaats aan het einde van een experiment om een objectieve maat te verkrijgen van het onderscheidend vermogen van de participant (zie bijv. Van den Bussche et al., 2009; Wenke et al., 2010). Tijdens deze taak wordt aan de participanten gevraagd om op de richting van de primes te reageren in plaats van op de target pijlen. Gebaseerd op de categorisatie van de primes (links versus rechts) kan er dan een d' (d prime) waarde worden berekend die dient als een directe maat voor prime zichtbaarheid. Deze maat is gebaseerd op de signaal detectie theorie (Green & Swets, 1966) en is een conservatievere evaluatie methode van prime zichtbaarheid dan bijvoorbeeld zelf rapportage (zie bijv. Cheesman & Merikle, 1986). Per participant wordt een gemiddelde d' waarde berekend die positief correleert met prime zichtbaarheid. Dat betekent dat een d'prime waarde van 0 perfecte onzichtbaarheid van de prime inhoudt en dat naarmate de zichtbaarheid toeneemt, ook de d' waarde stijgt. Wanneer de d'prime waarden niet significant van 0 afwijken, wordt aangenomen dat de primes voldoende subliminaal werden gepresenteerd.

Vrije keuzes in het Brein

Het is duidelijk dat subliminale primes een effect hebben op ons gedrag, het is echter minder duidelijk hoe subliminale primes activiteit in de hersenen beïnvloeden en welke hersengebieden betrokken zijn bij het verwerken van dit type onbewuste bottom-up informatie. Eerder onderzoek heeft reeds gekeken naar de functionele neuroanatomie van vrije keuzes, meestal door vrije keuzes te vergelijken met gecuede keuzes (Forstmann, Brass, Koch, & von Cramon, 2006; Demanet, De Baene, Arrington, & Brass, 2013; Orr & Banich, 2014). Een consistente bevinding is dat in ieder geval de rostral cingulate zone (RCZ), een deel van de mediale frontale cortex dat posterieur en dorsaal doorloopt vanuit de anterieure cingulate cortex (ACC), een rol speelt bij het maken van vrije keuzes (Figure 3). Naast de RCZ wordt het maken van vrije keuzes geassocieerd met activiteit in de dorsolaterale prefrontale cortex (DLPFC), anterieure insula (AI), pre-supplementaire motor cortex (pre-SMA), SMA, inferieure parietale lobule (IPL), en de frontopolaire cortex (FPC) (Forstmann et al., 2006; Demanet et al., 2013; Orr & Banich, 2014). Deze gebieden vormen samen een "keuze netwerk"



Figuur 3. Locatie van de rostral cingulate zone (RCZ). X coordinaat is 6.

dat deel uitmaakt van een omvangrijker vrijwillige actie netwerk (Spence, Hunter, & Harpin, 2002; Brass & Haggard, 2008; 2010; Brass, Lynn, Demanet, & Rigoni, 2013; Krieghoff, Waszak, Prinz & Brass, 2011; Lau, Rogers, & Passingham, 2006) dat eveneens overlapt met het zogenaamde *multiple demand* netwerk, waarin de verschillende onderdelen van complexe, intelligente mentale activateit worden gescheiden van elkaar, worden georganizeerd, opgeslagen en gecontroleerd (Duncan, 2010). Om intentioneel gedrag beter te kunnen verklaren, introduceerden Brass en Haggard (2008) het "Wat, Wanneer, Of" model (i.e. *Wat* te kiezen als respons? *Wanneer* deze respons uit te voeren? *Of* de respons moet worden uitgevoerd of niet?). Voor deze thesis is de 'Wat' component van dit model het belangrijkste, want deze component representeert de keuze die moet worden uitgevoerd. Er heerst nog steeds enige controverse omtrent de vraag welk hersengebied precies betrokken is bij het kiezen van een respons, maar wanneer hersenactiviteit wordt vergeleken tussen het maken van vrije keuzes en gecuede keuzes is de meest consistente bevinding dat de RCZ en de pre-SMA betrokken zijn bij dit proces (Lau, Rogers, Ramnani, & Passingham, 2004; Walton, Devlin, & Rushworth, 2004; Mueller, Brass, Waszak, Prinz, 2007). Tot nu toe werd aangenomen dat de RCZ een belangrijke rol speelt bij het kiezen tussen verschillende respons alternatieven (Forstmann et al., 2006; Demanet et al., 2013; Brass & Haggard, 2008; Cunnington, Windischberger, Robinson, & Moser, 2006; De Baene, Albers, & Brass, 2012; Lau et al., 2004; Mueller et al., 2007; van Eimeren et al., 2006; Venkatraman, Rosati, Taren, & Huettel, 2009; Walton et al., 2004). RCZ activiteit werd echter ook reeds gelinkt aan het oplossen van conflict in plaats van aan intentionele processen (Botvinick, Braver, Barch, Carter, & Cohen, 2001; Nachev, Rees, Parton, Kennard, & Husain, 2005). Dit impliceert dat activiteit in de RCZ gerelateerd is aan conflict tussen concurrerende respons alternatieven in plaats van daadwerkelijk aan het kiezen van de uiteindelijke respons. Aan de andere kant is competitie tussen verschillende respons alternatieven een cruciaal aspect van de 'wat' component (Botvinick et al., 2001; Nachev, Wydell, O'Neill, Husain, & Kennard, 2007), omdat de uiteindelijke keuze altijd de winnaar is van het conflict met de overige opties. In vrije keuze situaties zou deze competitie zelfs nog sterker kunnen zijn omdat er geen externe cues zijn om aan te geven welke keuze je dient te maken, waardoor de verschillende respons opties allemaal ongeveer evenveel gewicht hebben (Brass & Haggard, 2008). Wat betreft de pre-SMA hebben Sumner en collega's (2007) gevonden dat een patient met een specifieke lesie in dit gebied niet in staat was om concurrerende responsen te onderdrukken, wat impliceert dat de pre-SMA betrokken is bij de automatische onderdrukking van respons alternatieven die niet werden gekozen (Nachev et al., 2007; Brass & Haggard, 2008). Op basis van studies die geprobeerd hebben om respons conflict te scheiden van vrije keuzes kan worden gesteld dat er nog geen consesus is bereikt over dit onderwerp. Wat deze scheiding extra lastig maakt, is dat vrije keuze en conflict zo sterk samenhangen dat het wellicht niet eens mogelijk is om ze los van elkaar te bestuderen. Respons conflict zou een onlosmakelijke eigenschap van vrij handelen kunnen zijn en het kiezen tussen verschillende opties is dan noodzakelijk in deze situaties (Brass & Haggard, 2008).

Bottom-up en top-down invloeden gecombineerd

Het oplossen van conflict tussen verschillende alternatieven en het maken van vrije keuzes impliceert ook dat een bepaalde mate van top-down intentionele betrokkenheid nodig is, zelfs al vindt het conflict tussen de verschillende respons opties op onbewust niveau plaats. Desalnietemin is lang aangenomen dat subliminale priming een volledig automatisch proces was dat niet werd beïnvloed door bewuste, top-down processen (Posner & Snyder, 1975; Schneider & Shiffrin, 1977). Er zijn echter wel degelijk aanwijzingen dat top-down processen zoals aandacht, intenties en taak gerelateerde instructies een invloed hebben op hoe subliminale informatie wordt verwerkt (Kouider & Dehaene, 2007; Kiefer, 2007). Belangrijk om te vermelden is wel dat, aangezien bottom-up informatie onbewust kan worden waargenomen, modulatie door top-down processen in dat geval niet kan plaatsvinden in anticipatie op deze subliminale stimuli. In plaats daarvan verloopt de invloed van top-down processen in dat geval indirect middels de invloed van voorafgaande reacties, huidige intenties, of instructies die een bepaalde mind-set activeren (Kiefer, 2007). Met name aandacht is een belangrijke en zelfs cruciale voorwaarde voor subliminale priming. Wanneer er geen aandacht aan de primes meer wordt geschonken, verliezen ze ook hun invloed op ons gedrag (zie bijv. Dehaene et al. 1998; Naccache, Blandin, & Dehaene, 2002; Lachter, Forster, & Ruthruff, 2004; Kiefer, 2007). Naast aandacht zijn intenties een belangrijke top-down factor die een invloed heeft op hoe bottom-up informatie wordt verwerkt (Kiefer, 2007). Het concept 'intentie' is vrij breed en omvat bijvoorbeeld ook de bewuste representatie van het doel van een handeling en de toewijding aan dit doel om het te verwezenlijken (Ansorge & Neumann, 2005; Goschke, 2002; Kiefer, 2007). Het idee is dat subliminale primes enkel een invloed hebben wanneer ze een respons in gang zetten die past bij de huidige, geactiveerde intentie die iemand op dat moment heeft (Ansorge, Heumann, & Scharlau, 2002; Ansorge & Neumann, 2005; Eckstein & Perrig, 2007).

De neurale mechanismen van metacognitie

Gebaseerd op eerder onderzoek lijkt het tot dusver duidelijk dat top-down processen de invloed van subliminale bottom-up informatie kunnen moduleren. De vraag is uiteraard in hoeverre participanten directe controle hebben over conflict dat wordt veroorzaakt door subliminale stimuli? Kunnen participanten voelen dat er conflict is als de primes die dit conflict veroorzaken onbewust zijn? Recent onderzoek wijst uit dat dit mogelijk is middels een proces dat metacognitie heet (Desender, Van Opstal, & Van den Bussche, 2014; Desender, Van Opstal, Hughes, & Van den Bussche, 2016). Metacognitie refereert aan de subjectieve ervaringen die we hebben wanneer we een handeling uitvoeren. Een specifieke categorie binnen metacognitie is de ervaring van hoe vloeiend je een respons kan selecteren en uitvoeren. Om dit type metacognitie te bestuderen wordt deze ervaring van hoe vloeiend je een respons kan selecteren gemanipuleerd middels een subliminaal respons priming paradigma om een onbewust conflict te creëren tussen twee respons alternatieven. Aan de participanten wordt vervolgens na iedere trial gevraagd om aan te geven hoe moeilijk ze het vonden om snel en accurraat te reageren op de target stimuli. Zodoende wordt een metacognitief oordeel verkregen omtrent de moeilijkheid van de respons (Desender et al., 2014; 2016). Participanten gaven in eerder onderzoek aan dat ze incompatibele trials (waarin de prime interfereert met de correcte respons) moeilijker vonden dan compatibele trials, zelfs wanneer ze de primes niet konden waarnemen. Op neuraal niveau is het minder duidelijk wat er gebeurt, aangezien de neurale mechanismen achter de metacognitieve ervaring van respons conflict nog niet eenduiding zijn aangetoond. Een studie van Desender en collega's (2016) vond dat de subjectieve ervaring van de moeilijkheid tijdens het selecteren van een respons samenhangt met activiteit in de ACC (Van Veen & Carter, 2002; Ullsperger, Fischer, Nigbur, & Endrass, 2014; Jiang, Zhang, & van Gaal, 2015) die vaak wordt gelinkt aan respons competitie en conflict monitoring (Kiehl et al., 2000; van Veen, Cohen, Botvinick, Stenger, & Carter, 2001; Botvinick, Braver, Barch, Carter, & Cohen, 2001; Barch, Braver, Sabb, & Noll, 2000; Cohen, Botvinick, & Carter, 2000; MacDonald, Cohen, Stenger, & Carter, 2000; Botvinick, Nystrom, Fissell, Carter, & Cohen, 1999; Carter, Braver, Barch, Botvinick, Noll, &

Cohen, 1998; Carter, MacDonald, Botvinick, Ross, Stenger, Noll, & Cohen, 2000; Van Veen & Carter, 2002). De vraag is of de metacognitieve ervaring van moeilijkheid bij het kiezen van een respons en conflict los van elkaar kunnen worden gezien? Er zijn aanwijzingen dat dit mogelijk is. Zoals eerder werd vermeld, wordt conflict monitoring doorgaans in verband gebracht met activiteit in de ACC. fMRI onderzoek naar metacognitie daarentegen vond tot nu toe meestal dat de anterieure prefrontale cortex betrokken was bij metacognitie (Fleming & Dolan, 2012). De neurale mechanismen met betrekking tot de metacognitie van respons conflict zijn echter nog onduidelijk.

Overzicht van de hoofdstukken en belangrijkste resultaten

Ondanks pogingen van cognitieve neurowetenschappen en sociale psychologie ontbreekt het nog steeds aan een duidelijk overzicht van de processen die ten grondslag liggen aan het maken van vrije keuzes, met name omtrent de interactie tussen onbewuste bottom-up en bewuste top-down processen. Voor deze thesis hebben we een subliminaal respons priming paradigma gecombineerd met top-down manipulaties en data verzamel methodes zoals fMRI, met als doelstelling een aantal van de open vragen omtrent het maken van vrije keuzes te beantwoorden. In de eerste twee hoofdstukken ligt de focus op onbewuste bottom-up factoren en hoe deze het maken van vrije keuzes beïnvloeden. In hoofdstuk 3 hebben we gekeken naar hoe top-down processen samenhangen met bottom-up invloeden bij het maken van vrije keuzes. Tot slot hebben we in hoofdstuk 4 gekeken naar de neurale mechanismen achter de metacognitieve ervaring van respons conflict.

Hoofdstuk 1

Het eerste empirische hoofdstuk kijkt naar de invloed van bottom-up factoren op het maken van vrije keuzes en welke hersengebieden hierbij betrokken zijn. Eerder onderzoek heeft aangetoond dat de RCZ een cruciale rol lijkt te spelen bij het maken van vrije keuzes, echter de exacte functie van de

RCZ blijft een onderwerp van debat. Tijdens dit eerste experiment hebben we getracht om de rol van de RCZ bij het maken van vrije keuzes verder te verduidelijken door fMRI data te verzamelen van participanten die de respons priming taak uitvoerden. Net als voorgaand onderzoek vonden we dat activiteit in de RCZ samenhing met het maken van vrije keuzes. Daarnaast vonden we bij het maken van vrije keuzes ook activiteit in de anterieure insula, de dorsolaterale prefrontale cortex (DLPFC) en de pre-SMA. Zoals eerder reeds werd vermeld, maken deze hersengebieden deel uit van een ‘vrijwillige actie netwerk’ (Spence et al., 2002; Brass & Haggard, 2008; 2010; Brass et al., 2013; Krieghoff et al., 2011; Lau et al., 2006). De resultaten van hoofdstuk 1 tonen dat activiteit in een aantal gebieden binnen dit ‘vrijwillige actie netwerk’ kan worden gemoduleerd door subliminale informatie, met name in de RCZ en de anterieure insula. Op basis van deze resultaten stelden we voor dat de RCZ en anterieure insula beide betrokken waren bij het oplossen van conflict tussen verschillende respons alternatieven tijdens het maken van vrije keuzes. De resultaten van hoofdstuk 2 en 4 wijzen er echter erop dat deze interpretatie wel eens niet accuraat zou kunnen zijn, hierop kom ik terug bij het bespreken van de resultaten van deze hoofdstukken. Verder concludeerden we op basis van de resultaten van hoofdstuk 1 dat de DLPFC en de pre-SMA betrokken waren bij het uitvoeren van de gekozen respons.

Hoofdstuk 2

Een aantal studies hebben gekeken naar hersenactivatie voorafgaand aan het maken van vrije keuzes (Soon, Brass, Heinze, & Haynes, 2008; Soon, He, Bode, & Haynes, 2013). Deze studies gebruikten *multi-voxel-patroon-analyse* (MVPA) om te onderzoeken in hoeverre vrije keuzes reeds bepaald worden door processen die voorafgaan aan het maken van een bewuste keuze. Informatie op basis waarvan de keuze kon worden voorspeld, werd gevonden in de precuneus, frontopolaire cortex, pre-SMA en SMA. De conclusie die hieruit werd getrokken, was dat het inderdaad mogelijk was om de uiteindelijke keuze te voorspellen op basis van onbewuste intenties die voorafgaan aan de bewuste keuze (Soon et al. 2008). Echter, er is een alternatieve interpretatie die suggereert dat het niet onbewuste intenties zijn die werden gedecodeerd, maar eerder een bepaalde neiging, of *bias* in een bepaalde richting die uiteindelijke de keuzes beïnvloedde zonder dat dit intentioneel was (Bode et al. 2014). Het belangrijkste doel van dit hoofdstuk was om te onderzoeken hoe deze onbewuste *bias* het decoderen van respons alternatieven op basis van hersenactiviteit beïnvloedde. Hiervoor hebben we de data die werd beschreven in hoofdstuk 1 opnieuw geanalyseerd doormiddel van MVPA om te onderzoeken hoe onbewuste *bias* het coderen van respons alternatieven beïnvloedde bij zowel vrije als gecuede keuzes en of deze *bias* ook de decodering veranderde binnen de specifieke hersengebieden die reeds werden gerraporteerd door Soon en collega's (2008). Daarnaast wilden we ook onderzoeken of we respons alternatieven konden decoderen op basis van hersenactivatie in gebieden die eerder op basis van univariate fMRI analyses werden gevonden in relatie tot het maken van vrije keuzes. De resultaten van deze studie toonden dat het decoderen van respons alternatieven het beste lukte op basis van activatie in de precuneus, wat suggereert dat dit hersengebied gevoelig is voor de invloed van onbewuste *bias*. De resultaten suggereerden verder dat de precuneus wellicht als functie heeft informatie van externe en interne bronnen te integreren en te accumuleren wat dan leidt tot de uiteindelijke respons. In deze studie konden we de keuzes die mensen maakten niet voorspellen op basis van activatie in de RCZ en de anterieure insula, wat vragen oproept omtrent de betrokkenheid van de RCZ en de anterieure insula bij het verwerken van vrije keuzes en suggereert dat de vrije keuze gerelateerde activiteit die bij voorgaande studies in de RCZ werd gevonden eerder algemenere kenmerken van de taak reflecteert zoals moeilijkheid. We komen hierop terug in hoofdstuk 4.

Hoofdstuk 3

Een andere vraag die grotendeels onbeantwoord bleef, is in hoeverre bij het maken van vrije keuzes de verwerking van bottom-up factoren zoals subliminale primes gemoduleerd wordt door top-down factoren. Eerder onderzoek naar top-down invloeden op subliminale priming heeft nog niet gekeken naar vrije keuzes. Tot nu toe werd gekeken naar taken die duidelijke instructies en cues bevatten om aan te geven hoe participanten moesten reageren op bepaalde stimuli. Het is aangetoond dat een keuze die wordt beïnvloed door een top-down proces een bepaalde mate van intentionele betrokkenheid vereist, zoals bijvoorbeeld het besteden van aandacht aan de locatie waar de prime verschijnt of de instructies van de taak actief in het werkgeheugen houden. De vraag is wat er gebeurt wanneer, in de context van een vrije keuze, enkel de intentie van de participant wordt gemanipuleerd en aandacht voor de prime en de taakinstructies ongewijzigd blijven? De verwachting was dat in deze situatie het effect van de subliminale primes zou toenemen omdat er meer ruimte zou zijn voor de bottom-up informatie wanneer de top-down betrokkenheid zou afnemen. Om dit te onderzoeken combineerden we subliminale respons priming met een anti-vrije-wil-geloof manipulatie (zie bijv. Vohs & Schooler, 2008; Rigoni et al., 2011). In deze manipulatie leest de helft van de participanten een wetenschappelijke tekst waarin het bestaan van vrije wil in twijfel wordt getrokken. De andere helft van de participanten functioneert als controle groep en leest een wetenschappelijke tekst waarin vrije wil niet wordt vermeld. Participanten voerden vervolgens de respons priming taak uit zodat we de invloed konden onderzoeken van deze top-down manipulatie op de verwerking van de subliminale bottom-up informatie. Het idee was dat deze manipulatie het geloof in vrije wil zou doen afnemen en zodoende zou leiden tot minder intentionele betrokkenheid van de participanten en ze minder geneigd zouden zijn om vrij te kiezen. Hierdoor zouden de participanten gevoeliger voor de subliminale primes zijn en zou de bottom-up informatie dus een grotere inpact op het gedrag hebben. Cruciaal is wel dat de aandacht die aan de prime werd besteed onveranderd zou blijven door de manipulatie, zodat priming nog steeds kon plaatsvinden. De resultaten van hoofdstuk 3 lieten een significante afnamen zien van het geloof in vrij wil in de anti-vrije-wil groep. In deze groep zagen we een verhoogde gevoeligheid voor de primes in vergelijking met de controlegroep. Dit effect was enkel zichtbaar voor de vrije keuze conditie, niet voor de gecuede keuze conditie, wat aangeeft dat de gecuede keuze conditie niet of minder gevoelig was voor de manipulatie. Een mogelijke verklaringen voor deze bevindingen is dat de vrije wil manipulatie een afname van intentionele betrokkenheid tot stand heeft gebracht bij het maken van vrije keuzes.

Dit suggereert dat het doen afnemen van top-down betrokkenheid bij het maken van vrije keuzes meer ruimte geeft aan onbewuste bottom-up factoren om een invloed uit te oefenen. Deze resultaten ondersteunen het idee dat subliminale invloeden op ons gedrag niet volledig automatisch en oncontroleerbaar zijn, maar wel degelijk onder invloed staan van top-down facoren zoals onze intenties en overtuigingen over vrije wil bijvoorbeeld.

Hoofdstuk 4

In het laatste hoofdstuk wilden we kijken naar de subjectieve ervaring van subliminaal respons conflict, in het bijzonder naar de neurale basis van deze ervaring aangezien die nog grotendeels onbekend is. In dit experiment keken we naar hoe vloeiend je een respons kon selecteren terwijl we die respons selectie manipuleerden met subliminale respons priming. We vroegen na iedere trial aan de participanten hoe moeilijk ze het vonden om snel en accuraat te reageren op de target stimuli. Zodoende hadden we een metacognitieve maat die de subjectieve moeilijkheid reflecteerde bij het selecteren van de respons. In dit experiment werden enkel gecuede keuzes gebruikt aangezien tijdens een piloot studie participanten geen verschil in moeilijkheid aangaven tussen de vrije keuze condities (compatibel, incompatibel, neutraal). De beoordelingen van subjectieve moeilijkheid werden vervolgens gecorreleerd met hersenactiviteit om te zien welke hersengebieden samenhangen met dit subjectieve gevoel voor moeilijkheid en of dit dezelfde gebieden waren die ook gevoelig zijn voor respons conflict zoals de RCZ en de anterieure insula. De resultaten van hoofdstuk 4 laten zien dat participanten incompatibele trials waarin de prime interfreerde met de correcte respons als moeilijke ervaarden dan compatibele en neutrale trials. Dit effect vonden we eveneens terug in de RCZ en de anterieure insula. In deze gebieden vonden we een positieve correlatie tussen subjectieve moeilijkheid en hersenactivatie, wat aangeeft dat hersenactivatie toeneemt wanneer participanten het kiezen van de respons ook moeilijker vonden. Interessant is dat deze activatie werd gevonden zelfs wanneer we controlleerden voor prime-respons compatibiliteit en reactietijden. Deze bevinding ondersteunt samen met de bevindingen uit hoofdstuk 2 dat de RCZ en de anterieure insula waarschijnlijk niet enkel bij respons conflict actief zijn, maar ook of zelfs vooral een rol spelen bij het verwerken van meer algemene gedragsgerelateerde factoren zoals de subjectieve moeilijkheid van het selecteren en uitvoeren van de respons.

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Appendix

% Data Storage Fact Sheet
% Chapter 1
% Author: Martyn Teuchies
% Date: 29-08-2017

1. Contact details

1a. Main researcher

- name: Martyn Teuchies
- address: Henri Dunantlaan 2, 9000 Ghent, Belgium
- e-mail: Martyn.Teuchies@ugent.be

1b. Responsible Staff Member (ZAP)

- name: Prof. dr. Marcel Brass
- address: Henri Dunantlaan 2, 9000 Ghent, Belgium
- e-mail: Marcel.Brass@ugent.be

If a response is not received when using the above contact details, please send an email to data.pp@ugent.be or contact Data Management, Faculty of Psychology and Educational Sciences, Henri Dunantlaan 2, 9000 Ghent, Belgium.

2. Information about the datasets to which this sheet applies

* Reference of the publication in which the datasets are reported:

Teuchies, M., Demanet, J., Sidarus, N., Haggard, P., Stevens, M. A., & Brass, M. (2016). Influences of Unconscious Priming on Voluntary actions: role of the Rostral Cingulate zone. Neuroimage, 135, 243-252.

* Which datasets in that publication does this sheet apply to?:

The data sheet applies to all the data reported in chapter 1.

3. Information about the files that have been stored

3a. Raw data

* Have the raw data been stored by the main researcher? [X]YES/[]NO
If NO, please justify:

* On which platform are the raw data stored?
  - [X] researcher PC
  - [X] research group file server
  - [X] other (specify): external hard disk drive

* Who has direct access to the raw data (i.e., without intervention of another person)?
  - [X] main researcher

  - [X] responsible ZAP
  - [X] all members of the research group
  - [ ] all members of UGent
  - [ ] other (specify): ...

3b. Other files

* Which other files have been stored?
  - [X] file(s) describing the transition from raw data to reported results. Specify: See Method section Chapter 1

  - [X] file(s) containing processed data. Specify: files that contain the results of the first and second level fMRI analysis; Excel and SPSS files that contain processed behavioral data.

  - [X] file(s) containing analyses. Specify: See Method section Chapter 1; also SPM8 scripts used for analyses.

  - [X] files(s) containing information about informed consent
  - [ ] a file specifying legal and ethical provisions

  - [X] file(s) that describe the content of the stored files and how this content should be interpreted. Specify: A word file with an overview of the collected data and analyses.

  - [ ] other files. Specify: ...

* On which platform are these other files stored?
  - [X] individual PC
  - [X] research group file server
  - [X] other: external hard disk drive

* Who has direct access to these other files (i.e., without intervention of another person)?
  - [X] main researcher
  - [X] responsible ZAP
  - [X] all members of the research group
  - [ ] all members of UGent
  - [ ] other (specify): ...

4. Reproduction

* Have the results been reproduced independently?: [ ] YES / [X] NO

* If yes, by whom (add if multiple):
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  - address:
  - affiliation:
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```
% Chapter 2
% Author: Martyn Teuchies
% Date: 29-08-2017

1. Contact details
===========================================================

1a. Main researcher
-----------------------------------------------------------
- name: Martyn Teuchies
- address: Henri Dunantlaan 2, 9000 Ghent, Belgium
- e-mail: Martyn.Teuchies@ugent.be

1b. Responsible Staff Member (ZAP)
-----------------------------------------------------------
- name: Prof. dr. Marcel Brass
- address: Henri Dunantlaan 2, 9000 Ghent, Belgium
- e-mail: Marcel.Brass@ugent.be

If a response is not received when using the above contact details,
please send an email to data.pp@ugent.be or contact Data Management,
Faculty of Psychology and Educational Sciences, Henri Dunantlaan 2,
9000 Ghent, Belgium.


2. Information about the datasets to which this sheet applies
===========================================================
* Reference of the publication in which the datasets are reported:
Teuchies, M., Demanet, J., Wisniewski, D., & Brass, M. (Submitted).
The influence of subliminal primes on decoding response alternatives
from cued- and free-choices. Neuroimage.

* Which datasets in that publication does this sheet apply to?:

The data sheet applies to all the data reported in chapter 2.


3. Information about the files that have been stored
===========================================================
3a. Raw data
-----------------------------------------------------------

* Have the raw data been stored by the main researcher? [X]YES/[]NO
If NO, please justify:

* On which platform are the raw data stored?
  - [X] researcher PC
  - [X] research group file server
  - [X] other (specify): external hard disk drive

* Who has direct access to the raw data (i.e., without intervention
of another person)?
  - [X] main researcher
  - [X] responsible ZAP
  - [X] all members of the research group
  - [ ] all members of UGent
```

- [ ] other (specify): ...

3b. Other files

* Which other files have been stored?
  - [X] file(s) describing the transition from raw data to reported results. Specify: See Method section Chapter 1

  - [X] file(s) containing processed data. Specify: files that contain the results of the first and second level fMRI analysis; Excel and SPSS files that contain processed behavioral data.

  - [X] file(s) containing analyses. Specify: See Method section Chapter 1; also SPM8 scripts used for analyses.

  - [X] files(s) containing information about informed consent
  - [ ] a file specifying legal and ethical provisions

  - [X] file(s) that describe the content of the stored files and how this content should be interpreted. Specify: A word file with an overview of the collected data and analyses.

  - [ ] other files. Specify: ...

* On which platform are these other files stored?
  - [X] individual PC
  - [X] research group file server
  - [X] other: external hard disk drive

* Who has direct access to these other files (i.e., without intervention of another person)?
  - [X] main researcher
  - [X] responsible ZAP
  - [X] all members of the research group
  - [ ] all members of UGent
  - [ ] other (specify): ...

4. Reproduction

* Have the results been reproduced independently?: [ ] YES / [X] NO

* If yes, by whom (add if multiple):
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  - address:
  - affiliation:
  - e-mail:

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```
% Data Storage Fact Sheet
% Chapter 3
% Author: Martyn Teuchies
% Date: 29-08-2017

1. Contact details
===========================================================

1a. Main researcher
-----------------------------------------------------------
- name: Martyn Teuchies
- address: Henri Dunantlaan 2, 9000 Ghent, Belgium
- e-mail: Martyn.Teuchies@ugent.be

1b. Responsible Staff Member (ZAP)
-----------------------------------------------------------
- name: Prof. dr. Marcel Brass
- address: Henri Dunantlaan 2, 9000 Ghent, Belgium
- e-mail: Marcel.Brass@ugent.be

If a response is not received when using the above contact details,
please send an email to data.pp@ugent.be or contact Data Management,
Faculty of Psychology and Educational Sciences, Henri Dunantlaan 2,
9000 Ghent, Belgium.


2. Information about the datasets to which this sheet applies
===========================================================
* Reference of the publication in which the datasets are reported:
Teuchies, M., Demanet, J., & Brass, M. (In review). Reducing Belief
in Free Will Increases the Impact of Subliminal Information While
Making Free Choices. Consciousness and Cognition.

* Which datasets in that publication does this sheet apply to?:

The data sheet applies to all the data reported in chapter 3.


3. Information about the files that have been stored
===========================================================
3a. Raw data
-----------------------------------------------------------

* Have the raw data been stored by the main researcher? [X]YES/[]NO
If NO, please justify:

* On which platform are the raw data stored?
  - [X] researcher PC
  - [X] research group file server
  - [X] other (specify): external hard disk drive

* Who has direct access to the raw data (i.e., without intervention
of another person)?
  - [X] main researcher
  - [X] responsible ZAP
  - [X] all members of the research group
```

```
  - [ ] all members of UGent
  - [ ] other (specify): ...


3b. Other files
-----------------------------------------------------------

* Which other files have been stored?
  - [X] file(s) describing the transition from raw data to reported
results. Specify: See Method section Chapter 1

  - [X] file(s) containing processed data. Specify: files that
contain the results of the first and second level fMRI analysis;
Excel and SPSS files that contain processed behavioral data.

  - [X] file(s) containing analyses. Specify: See Method section
Chapter 1; also SPM8 scripts used for analyses.

  - [X] files(s) containing information about informed consent
  - [ ] a file specifying legal and ethical provisions

  - [X] file(s) that describe the content of the stored files and
how this content should be interpreted. Specify: A word file with an
overview of the collected data and analyses.

  - [ ] other files. Specify: ...

* On which platform are these other files stored?
  - [X] individual PC
  - [X] research group file server
  - [X] other: external hard disk drive

* Who has direct access to these other files (i.e., without
intervention of another person)?
  - [X] main researcher
  - [X] responsible ZAP
  - [X] all members of the research group
  - [ ] all members of UGent
  - [ ] other (specify): ...


4. Reproduction
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* Have the results been reproduced independently?: [ ] YES / [X] NO

* If yes, by whom (add if multiple):
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   - affiliation:
   - e-mail:


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% Data Storage Fact Sheet
% Chapter 4
% Author: Martyn Teuchies
% Date: 29-08-2017

1. Contact details

1a. Main researcher

- name: Martyn Teuchies
- address: Henri Dunantlaan 2, 9000 Ghent, Belgium
- e-mail: Martyn.Teuchies@ugent.be

1b. Responsible Staff Member (ZAP)

- name: Prof. dr. Marcel Brass
- address: Henri Dunantlaan 2, 9000 Ghent, Belgium
- e-mail: Marcel.Brass@ugent.be

If a response is not received when using the above contact details, please send an email to data.pp@ugent.be or contact Data Management, Faculty of Psychology and Educational Sciences, Henri Dunantlaan 2, 9000 Ghent, Belgium.

2. Information about the datasets to which this sheet applies

* Reference of the publication in which the datasets are reported: Teuchies, M., Desender, K., de Baene, W., Demanet, J., & Brass, M. (In preparation). Search your feelings: Neural correlates of the subjective experience of fluency in action-selection in a subliminal response priming task.

* Which datasets in that publication does this sheet apply to?:

The data sheet applies to all the data reported in chapter 4.

3. Information about the files that have been stored

3a. Raw data

* Have the raw data been stored by the main researcher? [X]YES/[]NO
If NO, please justify:

* On which platform are the raw data stored?
  - [X] researcher PC
  - [X] research group file server
  - [X] other (specify): external hard disk drive

* Who has direct access to the raw data (i.e., without intervention of another person)?
  - [X] main researcher
  - [X] responsible ZAP

- [X] all members of the research group
- [ ] all members of UGent
- [ ] other (specify): ...

3b. Other files

* Which other files have been stored?
  - [X] file(s) describing the transition from raw data to reported results. Specify: See Method section Chapter 1

  - [X] file(s) containing processed data. Specify: files that contain the results of the first and second level fMRI analysis; Excel and SPSS files that contain processed behavioral data.

  - [X] file(s) containing analyses. Specify: See Method section Chapter 1; also SPM8 scripts used for analyses.

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  - [X] file(s) that describe the content of the stored files and how this content should be interpreted. Specify: A word file with an overview of the collected data and analyses.

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  - [X] research group file server
  - [X] other: external hard disk drive

* Who has direct access to these other files (i.e., without intervention of another person)?
  - [X] main researcher
  - [X] responsible ZAP
  - [X] all members of the research group
  - [ ] all members of UGent
  - [ ] other (specify): ...

4. Reproduction

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  - address:
  - affiliation:
  - e-mail:

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