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Influences of unconscious priming on voluntary actions: Role of the rostral cingulate zone

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ABSTRACT

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

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 et al., 2006; Demanet et al., 2013; Orr and 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 et al., 2006; De Baene et al., 2012; Lau et al., 2004; Mueller et al., 2007; van Eimeren et al., 2006; Venkatraman et al., 2009; Walton et al., 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 and Banich, 2014). These regions form a “choice network” that is part of a larger voluntary action network (Spence et al., 2002; Brass and Haggard, 2008, 2010; Brass et al., 2013; Krieghoff et al., 2011; Lau et al., 2006). Another current research line focusses on whether or not voluntary choices are truly ‘free’ (Libet et al., 1982, 1983; Libet, 1985, 1999; Soon et al., 2008, 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 and Logan, 2005; Arrington et al., 2010; Wenke et al., 2010; Orr and Weissman, 2011; Orr et al., 2012; Demanet et al., 2013; Orr and Banich, 2014). Wenke et al. (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 and Banich, 2014). This research shows that some parts of the ‘choice network’ may be influenced by information that primes free choices.

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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 and 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 were done using Tscope software (Stevens et al., 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 17.94 ms (SD = 0.28). The response priming task was adapted from Chambon (Chambon et al., 2012). Three types of primes were used: gray colored 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 $0.8° \times 1.86°$, and the targets of $1.09° \times 3.47°$ (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) (Fig. 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 behavior. 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 1000 ms and 5250 ms. 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