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Neural signature of reward-modulated unconscious inhibitory control

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A B S T R A C T

Consciously initiated cognitive control is generally determined by motivational incentives (e.g., monetary reward). Recent studies have revealed that human cognitive control processes can nevertheless operate without awareness. However, whether monetary reward can impinge on unconscious cognitive control remains unclear. To clarify this issue, a task consisting of several runs was designed to combine a modified version of the reward-priming paradigm with an unconscious version of the Go/No-Go task. At the beginning of each run, participants were exposed to a high- or low-value coin, followed by the modified Go/No-Go task. Participants could earn the coin only if they responded correctly to each trial of the run. Event-related potential (ERP) results indicated that high-value rewards (vs. low-value rewards) induced a greater centro-parietal P3 component associated with conscious and unconscious inhibitory control. Moreover, the P3 amplitude correlated positively with the magnitude of reaction time slowing reflecting the intensity of activation of unconscious inhibitory control in the brain. These findings suggest that high-value reward may facilitate human higher-order inhibitory processes that are independent of conscious awareness, which provides insights into the brain processes that underpin motivational modulation of cognitive control.

1. Introduction

Motivation and cognition jointly determine human behavior. Higher performance-contingent rewards can generally facilitate cognitive control functions, including working memory (Heitz et al., 2008; Jimura et al., 2010; Taylor et al., 2004), conflict monitoring (Braem et al., 2014; Hubner and Schlosser, 2010; Padmala and Pessoa, 2011), task switching (Aarts et al., 2010; Capa et al., 2013; Kleinsorge and Rinkenauer, 2012), and inhibitory control (Boehler et al., 2012; Herrera et al., 2014; Leotti and Wager, 2010). Previous studies on the interface between reward and human performance support force-based theory (Atkinson and Birch, 1978; Berridge, 2004; Kruglanski et al., 2012). According to this theory, human action and performance are regarded as the result of forces (e.g., physical forces and mental effort), and cues of reward incentives are therefore deemed as driving forces. Consequently, people are driven to invest more effort, which contributes to improving behavioral performance when valuable rewards are at stake (Bijleveld et al., 2009; Capa et al., 2013). In contrast, increasing neuroscientific evidence emphasizes the interactive mechanisms of motivation and cognitive control (Beck et al., 2010; Dixon and Christoff, 2012; Kouneiher et al., 2009; Padmala and Pessoa, 2011). These studies have elucidated two interactive large-scale brain networks: one involved in mirroring the value of reward, including the prefrontal cortex (PFC) and a set of subcortical structures (e.g., ventral striatum, amygdala and the ventral tegmental area; Bartra et al., 2013; Liu et al., 2011; Miller and Cohen, 2001), and another implicated in cognitive functions, including the inferior frontal junction, the pre-supplementary area (pre-SMA), the dorsal anterior cingulate, and the superior parietal gyrus (Cole and Schneider, 2007; Niendam et al., 2012). The overlapping regions of the two networks contribute to behavioral and neural improvements of reward-induced cognitive processes (Botvinick and Braver, 2015; Chiew and Braver, 2011).

As stated previously, almost all approaches exploring this interaction have solely assessed the effect of reward on consciously initiated cognitive control, which may be affected by the traditional view that human cognitive processes depend on conscious awareness of task-relevant signals (Dehaene and Naccache, 2001; Eimer and Schlaghecken, 2002). However, recent research has demonstrated that higher-order cognitive control can also be triggered by unconsciously presented stimuli (Cohen et al., 2009; De Pisapia, 2013; Lau and Passingham,

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2007; van Gaal et al., 2008). For instance, inhibitory control, an essential component of cognitive functions in the human brain that denotes the inhibition of previously activated behavior and inappropriate actions, can also be triggered unconsciously (Chiu and Aron, 2014; van Gaal et al., 2010; Wokke et al., 2011). van Gaal et al. (2010) investigated the neural mechanisms of conscious and unconscious inhibitory controls simultaneously by developing a modified version of the Go/No-Go task consisting of conscious and unconscious Go/No-Go trials, with all trials displayed randomly. The unconscious Go/No-Go trials required participants to respond to an annulus (metacontrast mask, duration: 200 ms) preceded by a briefly presented white square (Go signal, duration: 16.7 ms) or diamond (No-Go signal, duration: 16.7 ms). In contrast, in conscious trials, participants were instructed to respond to a white square (duration: 200 ms) followed by an annulus (duration: 16.7 ms) but withhold their action to a white diamond (duration: 200 ms) followed by an annulus (duration: 16.7 ms). In fact, participants responded to almost all of the annuli in the unconscious trial condition because they failed to perceive the briefly presented Go and No-Go signals. Intriguingly, the authors observed that participants responded more slowly in unconscious No-Go trials than in unconscious Go trials, suggesting the existence of unconscious inhibitory control. The study also revealed that the inferior frontal cortex (IFC) and the pre-supplementary motor area (pre-SMA) are involved in both conscious and unconscious inhibitory control, suggesting that unconscious inhibitory control might share similar neural mechanisms with conscious inhibitory control. Nevertheless, it should be noted that conscious inhibitory control elicited stronger neural activation than unconscious inhibitory control in the IFC and pre-SMA. Thus, it is likely that conscious and unconscious cognitive processes may share similar mechanisms, with a different extent of activation in the same brain regions. Moreover, the behavioral index of unconscious inhibitory control, referred to as reaction time (RT) slowing (i.e., the difference between the mean RTs of unconscious No-Go trials and the mean RTs of unconscious Go trials), correlated positively with activation of the IFC and pre-SMA. This finding demonstrates that RT slowing could, in some sense, mirror directly the activation of human unconscious inhibition processes (Chiu and Aron, 2014; van Gaal et al., 2010; Xu et al., 2015).

Beyond the neuroimaging evidence, electrophysiological studies have explored the temporal dynamics of conscious and unconscious inhibitory control (van Gaal et al., 2011, 2008; Wokke et al., 2011). Specifically, both conscious and unconscious inhibitory controls have been associated with two event-related potential (ERP) components: a fronto-central component (negative peak around 250–350 ms after prime presentation) and a centro-parietal component (positive peak around 400–600 ms after prime presentation). Moreover, with respect to the N2 and P3 components, the prefrontal cortex (PFC) is assumed to play an essential role in the processing of conscious and unconscious inhibitory control. Nevertheless, even though both N2 and P3 are associated with PFC function, the dissociation of the two components must be emphasized. P3 is associated with inhibitory control (Albert et al., 2013; Bekker et al., 2005; van Gaal et al., 2008), whereas N2 is assumed to be related to the detection of response conflict (Donkers and van Boxtel, 2004; Enriquez-Geppert et al., 2010; Nieuwenhuis et al., 2003). Namely, it seems that P3 is the most essential neural signature of conscious and unconscious inhibitory control processes.

Although prior research has investigated the interface of reward and conscious inhibitory control, little research has addressed the link between reward and unconscious inhibitory control, as the unconscious inhibitory control has been thought to play an essential role in monitoring and filtering the surge of unconsciously presented information in our daily lives (Suhler and Churchland, 2009; van Gaal et al., 2010). More importantly, the neural mechanisms underlying the interaction between reward and unconscious inhibitory control remain unclear. In this study, we used ERPs to investigate this issue with a cognitive task combined with a modified version of the reward-priming paradigm and a modified version of Go/No-Go task. Given the empirical evidence mentioned previously, we hypothesized that participants would expend more mental effort for high-value rewards than low-value rewards, as explained by force-based theory. Moreover, we hypothesized that reward-induced performance improvements in control, especially at the neural level, would be observed in both conscious and unconscious inhibitory control conditions. Specifically, high-value rewards (vs. low-value rewards) would facilitate conscious and unconscious inhibition processes, as shown by a greater centro-parietal P3 component, strongly supporting a prior view on the interactive neural mechanisms underlying reward value and cognitive control.

2. Methods

2.1. Participants

Eighteen undergraduates from Southwest University of China participated in this study (18–23 years; mean age 21.6; 10 female). All participants were right-handed with normal or corrected-to-normal vision. This research was executed in compliance with relevant laws and was approved by the Ethics Board of Southwest University. Written informed consent was obtained from all participants before the experiment. When they finished the experiment, participants received any money they earned in the experiment. On average, participants earned 10.75 yuan RMB ($SD = .91$; Maximal earnings = 12.11 yuan; Minimal earnings = 9.07 yuan).

2.2. Stimuli and procedure

Stimuli were displayed against a black background (2.17 cd/m^2) at the center of a 20-inch Dell monitor (Dell, Inc., Round Rock, Texas) with 60-Hz refresh rate, using E-prime software (Psychology Software Tools, Inc., Sharpsburg, PA). Participants sat in a dimly lit room and viewed the monitor from a distance of about 70 cm so that each centimeter subtended a visual angle of 0.82°.

A modified version of the reward-priming paradigm was adapted from Pessiglione et al. (2007), and a modified version of the Go/No-Go task was adapted from van Gaal et al. (2010). In this experiment, participants performed an initial practice run and 24 experimental runs. Each run began with a fixation cross presented for 2500 ms, followed by a pre-blank (300 ms), a coin (1000 ms), a post-blank (300 ms), and the modified Go/No-Go task of 32 successive trials. Participants were informed that the value of the coin could be 1 cent or 1 yuan RMB (approximately 100 cents). They were instructed to respond to the Go/No-Go task as quickly and accurately as possible and were informed that they could earn the coin preceding the Go/No-Go task when they responded correctly to each trial of the run. The cumulative earnings were presented on the last screen of each run (Fig. 1).

Each run of the Go/No-Go task in this experiment consisted of 32 trials, divided into four trial types (conscious Go trials, conscious No-Go trials, unconscious Go trials, and unconscious No-Go trials), with eight trials for each trial type. The conscious trials and unconscious trials were intermixed. Participants were informed to press the “*m*” key to a white annulus (visual angle of 0.8°) as quickly and accurately as possible with their right index finger. However, they needed to inhibit their response when a white square (the No-Go signal, visual angle of $0.47° \times 0.47°$) preceded the annulus. Additionally, participants were instructed to “keep on going” and press the “*m*” key when a white diamond (the Go signal, the same square revolved by 45°) preceded the annulus. In this experiment, the Go and No-Go signals were counterbalanced among participants.

On conscious Go/No-Go trials, the Go/No-Go signals were presented for 233 ms and the annulus for 17 ms. On unconscious Go/No-Go trials, the Go/No-Go signals were presented for 17 ms and the annulus for 233 ms. It should be noted that the annulus acted as a metacontrast mask in the unconscious trial condition, as it could effectively reduce stimulus visibility (Breitmeyer et al., 1984). Participants could therefore