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Neural correlates of the Simon effect modulated by practice with spatial mapping

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ABSTRACT

The operation of cognitive control relies on existing stimulus–response (S–R) mapping rules in the brain. However, it remains unclear how a newly acquired S–R mapping rule (i.e., learning) may alter the cognitive control system. We examined this question with functional magnetic resonance imaging and the Simon effect influenced by preceding practice. Behavioral results revealed a reversed Simon effect following practice with incompatible spatial location mapping (experimental group; $n=20$) but a classic Simon effect in the group with compatible location mapping practice (control group; $n=20$). Neuroimaging results showed reduced activity in the anterior midcingulate cortex (aMCC) and increased functional coupling between the aMCC and the right frontopolar cortex (FPC) in the experimental group compared to the control group. The bilateral temporoparietal junction responded more to the stimuli that matched a task configuration related to prior practice. In addition, the functional circuit of the right FPC-ventral premotor cortex (vPMC) correlated with the Simon effect influenced by prior practice, suggesting that the FPC-vPMC pathway might represent the abstract response rule acquired during practice and applies the rule to modify behavior. Collectively, these findings reveal how the brain represents previously learned response rules and subsequently modifies the cognitive control system.

1. Introduction

Cognitive control refers to the ability to coordinate cognitive processes to adapt one's behavior according to current goals (Miller & Cohen, 2001). Human neuroimaging and computational modeling studies have shown that control processes are primarily subserved by prefrontal cortex (PFC) (Botvinick, Braver, Barch, Carter, & Cohen, 2001; Egner & Hirsch, 2005; Kerns et al. 2004; MacDonald, Cohen, Stenger, & Carter, 2000). In addition, it has been suggested that prefrontal cortex is hierarchically organized along rostral-caudal axis, with more anterior regions providing control signals at a higher abstract level for actions (Badre, 2008; Badre & D'Esposito, 2007; Koechlin, Ody, & Kouneiher, 2003; Koechlin & Summerfield, 2007; O'Reilly, 2010). Furthermore, Badre Kayser and D'Esposito(2010) showed that the more anterior PFC region representing higher abstract rules was also involved in learning abstract rules. More recently, the relationship between learning and cognitive control in the brain has been investigated not only because they share common neural substrates but also because of its important theoretical implications (Badre & Frank, 2012; Collins & Frank, 2013; Frank & Badre, 2012). For example, how does the cognitive control system operate after learning new stimulus–response (S–R) associations? In a typical cognitive control task, overlearned but task-irrelevant S–R mappings (e.g., reading a printed word in the Stroop task or responding to the source of stimulus in the Simon task) may interfere with the task-relevant S–R mapping (Cohen, Dunbar, & McClelland, 1990; Lu & Proctor, 1995). It has been established that medial (e.g., anterior cingulate cortex, ACC/anterior midcingulate cortex, aMCC) and lateral (e.g., dorsolateral PFC, DLPFC) PFC regions are involved in initiating and implementing the control processes to overcome interference (Blais & Bunge, 2010; Botvinick, Nystrom, Fissell, Carter, & Cohen, 1999; Carter et al., 2000; Desmet, Fias, Hartstra, & Brass, 2011; Egner & Hirsch, 2005; Kerns et al., 2004; MacDonald et al., 2000). In other words, the cognitive control system functions in terms of existing S–R mapping rules in the brain. For instance, specifically in the Simon task, the response conflict evoked by irrelevant spatial S–R and relevant non-spatial S–R associations may be detected by ACC/aMCC and then trigger subsequent control processes (Fan, Flombaum, McCandliss, Thomas, & Posner, 2003; Liu, Banich, Jacobson, & Tanabe, 2004; Peterson et al., 2002; Wittfoth, Buck, Fahle, & Herrmann, 2006). However, it is unclear how a newly acquired S–R association (i.e., learning) alters

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the cognitive control system. We explored this question using functional magnetic resonance imaging (fMRI) in the present study.

The Simon effect is a classic behavioral paradigm used to investigate cognitive control in laboratory studies (Botvinick, Cohen, & Carter, 2004; Hommel, 2011b). It refers to the finding that reaction time (RT) is shorter when the spatial location of a stimulus corresponds to the location of response (i.e., congruent condition) than when it does not (i.e., incongruent condition), although the spatial information of stimuli is irrelevant to the task performed (C. H. Lu & Proctor, 1995; Simon, 1990; Simon & Rudell, 1967; Simon & Small, 1969). A widely accepted dual-route model has been proposed to explain the mechanism underlying the Simon effect (Barber & OLeary, 1997; De Jong, Liang, & Lauber, 1994; Kornblum, Hasbroucq, & Osman, 1990; Zhang, Zhang, & Kornblum, 1999; Zorzi & Umilta, 1995). The task-relevant (non-spatial) attribute of the stimulus (e.g., color) activates the correct response representation defined by a short-term-memory S–R association (conditional). In addition, the spatial information of the stimulus activates its spatially corresponding response representation via a long-term-memory S–R association (unconditional). If the two associations activate different response representations, the incorrect representation evoked by the unconditional route has to be inhibited in favor of the correct one, resulting in slower RT. The Simon effect is therefore attributed to interference in response selection processes (Hommel, 2011b), and reflects the influence of an irrelevant S–R association on the relevant S–R association. However, it is still under debate how spatial codes of stimuli are formed in the Simon task. One possibility is that the spatial codes are generated by attention-shifts towards the spatial location of stimulus (Abrahamse & Van der Lubbe, 2008; Nicoletti & Umilta, 1994; Van der Lubbe & Abrahamse, 2011; Van der Lubbe, Abrahamse, & De Kleine, 2012). An alternative view is that the spatial codes are triggered by the actual location of stimulus (Hommel, 1993, 2011a).

In terms of how learning new S–R associations alter the cognitive control system, it has been demonstrated that the interference effect in the Simon task can be reduced or even reversed by long-term practice (Proctor & Lu, 1999; Proctor, Yamaguchi, Zhang, & Vu, 2009; Tagliabue, Zorzi, Umilta, & Bassignani, 2000; Vu, 2007). For instance, after practice with incompatible location mapping (e.g., left stimulus-pressing right key; right stimulus-pressing left key) for 72 trials, the Simon effect is eliminated (Tagliabue et al., 2000) and with more practice (e.g., 1800 trials) it is significantly reversed (Proctor & Lu, 1999). One account of this effect suggests that the short-term-memory (STM) S–R associations formed in prior practice with incompatible location mapping remain effective and interact with the task-defined S–R associations in the Simon task, resulting in the elimination or reversal of the Simon effect (Tagliabue et al., 2000). The cross-dimension practice effects on the Simon effect further suggest that the STM S–R associations could also reflect a transfer effect at a higher abstract level (Treccani, Milanese, & Umilta, 2010; Vu, 2007). In addition, recent studies have revealed that the long-term practice effect and the trial-by-trial sequential effect (Botvinick et al., 1999; Gratton, Coles, & Donchin, 1992; Kerns et al., 2004) are independent of each other (Iani, Rubichi, Gherri, & Nicoletti, 2009; Soetens, Maetens, & Zeischka, 2010), suggesting that neural circuits different from the aMCC-DLPFC pathway are engaged in the practice modulated Simon effect. The trial-by-trial sequential effect refers to the modulation of the interference effect by the congruency of proceeding trials (Ullsperger, Bylsma, & Botvinick, 2005). The frontopolar cortex (FPC) locates at the apex of the rostrocaudal, abstract-to-concrete hierarchical gradient of PFC. It has an established role in holding information in working memory when switching between tasks and also when representing abstract task rules (Badre & D'Esposito, 2007; Koechlin, Basso, Pietrini, Panzer, & Grafman, 1999; Ramnani & Owen, 2004). In addition, it was suggested that FPC could exert higher level control over posterior PFC regions to guide actions (Koechlin & Summerfield, 2007). Here, we used fMRI to test the hypothesis that the interaction between FPC and posterior PFC regions (e.g., premotor areas) underlies the practice modulated Simon effect. At the behavioral level, we predicted that the Simon effect would be reversed by practice with incompatible spatial location mapping.

2. Material and methods

2.1. Participants

Forty healthy participants (17 female, mean age = 24.9 years, range = 18–35 years) with no history of psychiatric, neurological or orthopedic disorder were recruited and paid for their participation in the study. They were randomly assigned to one of the two conditions: experimental group ($n = 20$, 7 female, mean age $\pm$ SD = 25.6 ± 5.1 years) and control group ($n = 20$, 10 female, mean age $\pm$ SD = 24.1 ± 3.5 years). All were right-handed according to self-report. Their vision was normal or corrected-to-normal. All participants gave informed consent. Each of them was paid 150 HKD for their participation. The study was approved by the local Human Ethics Committee of the University of Hong Kong.

2.2. Apparatus and stimuli

Visual stimuli were displayed on a screen at the rear end of the scanner bed through an LCD projector (EMP-1710, EPSON, Suwa, Nagano, Japan), visible via a mirror mounted on the headcoil. All visual stimuli were generated using Presentation software (Neurobehavioral Systems, Albany, CA, USA). The background of the visual stimuli was black. A white cross hair (visual angle: 1.0° vertical × 1.0° horizontal) in the screen center served as a fixation point. The target stimulus was a circle (1.0° vertical × 1.0° horizontal) in red (RGB values: 255, 0, 0), green (RGB values: 0, 255, 0), or white (RGB values: 255, 255, 255), which was displayed randomly on the left (visual angle between the fixation cross and the stimulus: 0° vertical × 3.3° horizontal) or right (0° vertical × 3.3° horizontal) side of the screen. Two MRI-compatible response pads with fiber optic cables were placed beside the left and right thigh of participants, respectively. Participants held the response pads with their hands and pressed the key on the left pad (hereafter the left key) or the key on the right pad (hereafter the right key) with their left or right thumb to respond to target stimuli.

All MRI images were acquired with a Philips Achieva3-T scanner (Best, the Netherlands) in the Department of Diagnostic Radiology at the University of Hong Kong. We used a gradient echo planar imaging (EPI) sequence to acquire fMRI data with the following parameters: repetition time (TR) = 2000 ms, echo time (TE) = 30 ms, field of view (FOV) = 240 mm, 32 axial slices, slice thickness = 3.0 mm, slice gap = .75 mm, in-plane resolution = 3.0×3.0 mm^2, and flip angle = 90°. The first 4 volumes were discarded to allow for T1 equilibration effects. Additional high-resolution anatomical images (voxel size = $1 \times 1 \times 1$ mm^3) were acquired using a standard T1-weighted 3-D Magnetization-Prepared Rapid Gradient-Echo (MP-RAGE) sequence. Images were analyzed using the Statistical Parametric Mapping (SPM) software (SPM8; Wellcome Trust Centre for Neuroimaging, University College London, London, UK).

2.3. Procedure

Each participant carried out three sessions of tasks successively. In the first (baseline) session, subjects performed a red-green color