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Functional imaging of brain responses to different outcomes of hypothesis testing: revealed in a category induction task

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ABSTRACT

Functional magnetic resonance imaging (fMRI) was used to examine differences in brain activation that occur when a person receives the different outcomes of hypothesis testing (HT). Participants were provided with a series of images of batteries and were asked to learn a rule governing what kinds of batteries were charged. Within each trial, the first two charged batteries were sequentially displayed, and participants would generate a preliminary hypothesis based on the perceptual comparison. Next, a third battery that served to strengthen, reject, or was irrelevant to the preliminary hypothesis was displayed. The fMRI results revealed that (1) no significant differences in brain activation were found between the 2 hypothesis-maintain conditions (i.e., strengthen and irrelevant conditions); and (2) compared with the hypothesis-maintain conditions, the hypothesis-reject condition activated the left medial frontal cortex, bilateral putamen, left parietal cortex, and right cerebellum. These findings are discussed in terms of the neural correlates of the subcomponents of HT and working memory manipulation.

Introduction

Hypothesis testing (HT) is a form of high order cognition that occurs when a hypothesis is alternatively confirmed or rejected under different types of evidence (Bruner et al., 1956). It is the basis of rule-based category learning, decision-making, and problem solving (Ashby and Maddox, 2005; Bruner et al., 1956; Filoteo et al., 2005; Shye, 1988; Wason, 1968).

In recent decades, several studies employed multi-trial learning tasks in different paradigms to reveal the neural basis of HT (Elliott and Dolan, 1998; Monchi et al., 2001; Seger and Cincotta, 2006; Strange et al., 2001). For example, Elliott and Dolan (1998) presented participants with a complex nonverbal task during which they attempted to determine a rule governing which of 2 checkerboard patterns was correct. Positron emission tomography revealed that HT activated the cerebellum, left anterior cingulate cortex (ACC), right precuneus, right thalamus, and left inferior frontal gyrus. Although this study explored brain areas that were associated with the process of HT, the task was unsolvable, and the hypotheses generated by participants were unclear. In addition, the task included hypothesis generation and HT. Therefore, it is unclear which sub-process was related to the observed brain activation.

In a rule induction task, Strange et al. (2001) asked subjects to categorize letter strings as "grammatical" or "ungrammatical" according to a currently relevant rule. The functional magnetic resonance imaging (fMRI) data showed that the bilateral anterior prefrontal cortices (PFC) were selectively engaged following a rule change (i.e., an old rule/hypothesis was rejected and a new rule was formed). Similarly, Seger and Cincotta (2006) found brain activity in the striatal, frontal, and hippocampal systems during a rule-learning task that requiring HT. Monchi et al. (2001) used the Wisconsin Card Sorting Task, in which the core processes are hypothesis generation and HT. They found that the negative feedback to participant's response, but not positive feedback, activated the prefrontal–cortical–basal ganglia loop, including the mid-ventrolateral PFC, caudate nucleus, mediodorsal thalamus, right prestriate cortex, left lateral premotor cortex, and right posterior parietal cortex. Although the authors examined HT-related feedback, they were unable to separate the relative contributions of HT and hypothesis generation (Monchi et al., 2001). Specifically, when negative feedback was displayed, participants might immediately shift to other perceptual dimensions and generate a new hypothesis (i.e., matching criteria) simultaneous to their rejection of the preliminary hypothesis (Konishi et al., 2003; Owen et al., 1991).

The experimental tasks used in previous relevant studies were multi-trial learning tasks. When a preliminary hypothesis or rule was rejected in a trial, the participants were asked to generate a new rule for the subsequent trials. Accordingly, the neural activity associated with HT could not be separated from that related to hypothesis generation.

The purpose of the present study was to isolate the process of HT and directly investigate its neural correlates. We employed a single-trial category induction task, which was recently used to assess scalp potentials for different HT outcomes (Li et al., 2009a, 2009b,

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2011). Participants were shown 3 figures of batteries and were asked to learn a rule regarding what kinds of batteries were charged. First, they were presented sequentially with two charged batteries that shared one common attribute (rectangular shape in Fig. 1). Participants could form a preliminary hypothesis (e.g., those rectangular batteries are charged) after inducing a category based on the perceptual comparison of both stimuli (Bigman and Pratt, 2004; Li et al., 2009a, 2009b). They were then presented with a third battery, which might change (strengthen/reject) the preliminary hypothesis. Alternatively, the third image could be irrelevant and the hypothesis remained unvarying. As shown in Fig. 1, participants completed the rule-learning task within a single trial. In the hypothesis-reject condition, participants should abandon the preliminary hypothesis upon presentation of the third battery, which functioned as negative feedback. Because it was a single trial, they did not shift to other perceptual dimensions when a preliminary hypothesis was rejected.

Based on results from previous event-related potential (ERP) (Li et al., 2009a, 2009b, 2011; Cai et al., 2011) and fMRI studies on HT (Elliott and Dolan, 1998; Monchi et al., 2001; Seger and Cincotta, 2006; Strange et al., 2001), we predicted that the different results of HT might generate brain activity in different cerebral cortices. Specifically, when a hypothesis was rejected, the stimulus would conflict with the preliminary hypothesis, which would not be maintained in working memory (WM). Accordingly, transient process of conflict monitoring and WM manipulation would occur in this condition, and the WM-related brain activation in the frontal cortex would be expected to increase markedly (Andreasen et al., 1992; Baker et al., 1996; Cohen et al., 1997; Goldberg et al., 1998; Monchi et al., 2001; Owen et al., 1996; Petrides et al., 1993).

In addition, WM manipulation during the hypothesis-reject condition accompanies with the updating of cognitive context. Previous studies demonstrated that the anterior PFC and basal ganglia, including the caudate and putamen, were involved in the updating process (Burgess et al., 2007; Seger and Cincotta, 2006). Therefore, we predict that these brain areas might also be recruited in the process of rejecting a hypothesis.

Methods

Participants

17 undergraduates took part in this experiment (9 males, 8 females; mean age: 20) and were paid for participation. Subjects met criteria for magnetic resonance imaging (MRI) scanning (no metallic implants, no claustrophobia, head size compatible with the custom head coil) and were neurologically healthy (no known neurological or psychiatric injury or disease, not taking any psychoactive medication or drugs). They were right-handed individuals and had normal or corrected-to-normal eyesight without color blindness. All participants provided written informed consent.

Materials and task

Images of batteries (6×3 cm) were sequentially displayed in the center of a 17-in. screen. Within each trial, the batteries varied in either shape (rectangle, oval, trapezoid, pentagon, or rhombus) or color (red, yellow, green, blue, or purple). Variation in shape or color was randomized across trials. A light bulb was placed above each battery, which was light gray (25% gray) in color if the battery was charged and dark gray (75% gray) if the battery was uncharged (Fig. 1). The horizontal visual angles subtended by batteries were less than 3°, and the vertical visual angles were not more than 4°. The horizontal and vertical visual angles subtended by light bulbs were less than 1°.

Participants were informed that some batteries were charged and others might not be; their task was to learn which batteries were charged. Within each trial, the first 2 batteries were both charged and shared a common attribute so that participants could form a hypothesis. After the presentation of the first 2 charged batteries (S1

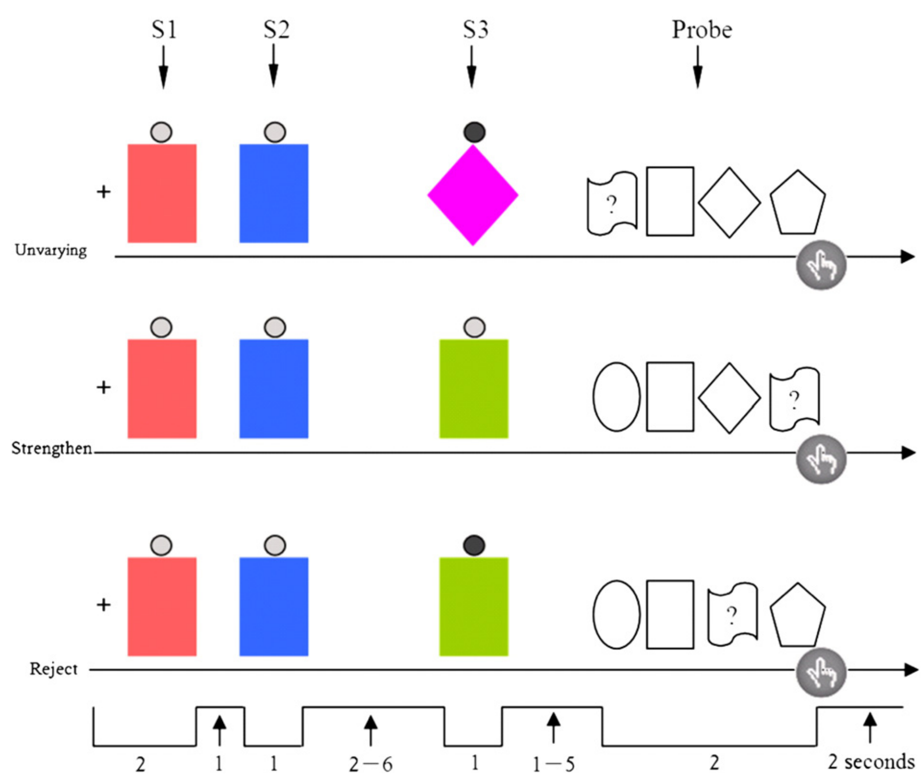

Fig. 1. Overall design and procedure of task with sample stimuli.