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Reward value enhances post-decision error-related activity in the cingulate cortex

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ABSTRACT

By saying “Anyone who has never made a mistake has never tried anything new”, Albert Einstein himself allegedly implied that the making and processing of errors are essential for behavioral adaption to a new or changing environment. These essential error-related cognitive and neural processes are likely influenced by reward value. However, previous studies have not dissociated accuracy and value and so the distinct effect of reward on error processing in the brain remained unknown. Therefore, we set out to investigate this at various points in decision-making. We used functional magnetic resonance imaging to scan participants while they completed a random dot motion discrimination task where reward and non-reward were associated with stimuli via classical conditioning. Pre-error activity was found in the medial frontal cortex prior to response but this was not related to reward value. At response time, error-related activity was found to be significantly greater in reward than non-reward trials in the mid-cingulate cortex. Finally at outcome time, error-related activity was found in the anterior cingulate cortex in non-reward trials. These results show that reward value enhances post-decision but not pre-decision error-related activities and these results therefore have implications for theories of error correction and confidence.

1. Introduction

The detection and prevention of errors in everyday decision-making can save time and can aid in communication. For example, imagine sending an important email and forgetting the attachments. The sooner you detect this error, the sooner you can rectify it by sending a new email with the attachments included (”error correction”; e.g. Hochman et al., 2015). This experience might help you learn to be more careful when sending emails in the future (see Holroyd and Coles, 2002). This type of behavioral adjustment is paramount for adaption to a dynamic environment, and according, there has been extensive research into the detection and monitoring of errors subsequent to their making.

Classic experiments into error processing showed that even without receiving explicit feedback on their performance people are often very capable of detecting and correcting their errors (Rabbitt, 1966; Rabbitt and Vyas, 1981). Subsequent neuroimaging studies have investigated which areas of the brain monitor or detect error responses. The medial frontal cortex (MFC), including the anterior cingulate cortex (ACC), has been shown to be active after errors (Carter et al., 1998; Kiehl et al., 2000; Carter et al., 2001; Menon et al., 2001; Garavan et al., 2002; Mathalon et al., 2003; Kerns et al., 2004; Iannaccone et al., 2015); it thus appears to be involved in the post-decision processing of error (Scheffers et al., 1996; Coles et al., 2001). Further evidence is provided by the error-related-negativity (ERN) and feedback ERN. These are components of encephalography measured from fronto-central sites generated in the MFC, most likely in the ACC (Dehaene et al., 1994; Miltner et al., 1997; Stemmer et al., 2004). The ERN has been shown to consistently peak after erroneous responses and the feedback ERN has been shown to consistently peak after feedback that reveals that the selected option was wrong (Falkenstein et al., 1991; Gehring et al., 1990; Miltner et al., 1997). It was recently proposed that as well as contributing to post-response and post-feedback error processing, activity in the ACC prior to response might also affect whether or not the response is erroneous (Hoffman & Beste, 2015).

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The ACC is tightly related to the mesencephalic dopamine system (Gaspar et al., 1989; Berger et al., 1991; Williams and Goldman-Rakic, 1993), which is a major part of the reward processing system (e.g. Schultz et al., 1997; Bayer and Glimcher, 2005). Therefore, it is in a unique position where it might be able to combine error and reward processing. In fact, several studies have shown that reward value enhances ACC error-related neural activity that occurs immediately after response (Hajcak et al., 2005; Schlienz et al., 2013). However, in these studies, the participants were rewarded only for correct responses and therefore response was confounded with outcome. It is thus elusive whether ACC error-related neural activity is distinctively affected by reward value or if combined processing of error and value only occurs in the ACC when response and outcome are associated via instrumental learning.

In this functional magnetic resonance imaging study, we tested to see if reward value, even when dissociated from response, enhances error processing. We scanned participants while they performed a random dot-motion direction discrimination task where reward and non-reward were associated with stimuli via classical conditioning. Regardless of whether participants responded correctly or not, they always received a reward after dot-motion in one direction (e.g. left) and a neutral outcome after dot-motion in the other direction (e.g. right). This allowed us to test neural activity in rewarded error and non-rewarded correct trials as well as in rewarded correct and non-rewarded error trials, and therefore to separately examine the effects of perceptual accuracy and reward value. Because error-related processing in the MFC has been found or suggested to occur at several stages of processing, we investigated neural activities for error and value processing at three different time periods: during stimulus presentation prior to response, at response time, and when the outcome was delivered.

2. Materials and methods

2.1. Ethics statement

All participants were informed about what this study would require from them. They completed written consent forms before the experiment. This study was approved by the ethics committee of Brain Science Institute of Tamagawa University.

2.2. Participants

Eighteen neurologically and psychologically healthy, right-handed, undergraduate students (nine female, nine male, mean age 20 ± 1.2 years; this style indicates mean $\pm$ s.d.) participated in this experiment after which they were compensated with a total of 7,000 yen. Participants were asked to refrain from eating for at least 10 h before the beginning of the experiment so as to maximize the value of the juice reward. When required, participants were provided with MRI-compatible eyeglasses of the necessary strength. Data of nine other participants were excluded from analyses due to excessive motion or low error rates.

2.3. Materials

Visual stimulus presentation was controlled using the “psychophysics toolbox” (Brainard, 1997) running on Matlab 7.1 (Mathworks, Inc.). The visual stimuli were projected to an opaque screen set inside the scanner via a (CP-SX1350, HITACHI; frame rate = 60 Hz) projector and a mirror system. Participants responded to the stimuli using MRI compatible response pads (HHSC-2 $\times$ 2, Current Designs, Inc., PA, USA).

2.4. Experimental procedure

Each participant completed the tasks over a consecutive two-day period. Rating of the liquids as well as practice, psychophysical testing, and conditioning were all completed on the first day (see the supplementary materials). On the second day, further conditioning (described in the supplementary materials) was completed. During the conditioning, participants were faster to respond in trials were dots moved in the reward-associated direction (0.58 ± 0.04 s) than in trials where dots moved in the non-reward-associated direction (0.60 ± 0.04 s; t_{17} = -2.34, $p < 0.05$). This indicates that participants successfully learned to associate one direction with reward and the other direction with non-reward. The main task was completed immediately after conditioning on the second day. Liquids were used as reward and non-reward stimuli. Participants rated these before and after the experiment. Each participant’s most preferred of the following was used as their reward liquid: apple juice, orange juice, or a popular Japanese yoghurt flavored drink (Calpis co.). These shall hereby be referred to as “juice”. On a scale ranging from −5 (I don’t like it at all) to +5 (I like it very much), the most preferred of these was rated before the experiment with a mean of 4.3 (s.d. = 0.8) and after the experiment with a mean of 3.1 (s.d. = 1.7). To make a neutral tasting control similar in content to human saliva (O’Doherty et al., 2002), ions and water were mixed in different concentrations (25 mM KCL and 2.5 mM NaHCO3 $\times$ 1, 2 or 3, with 1 liter of water). These shall hereby be referred to as “ion water” solutions. Each participant’s most neutrally rated of these solutions was used as their non-reward liquid. On the same scale ranging from −5 to +5, the most neutrally rated ion water solutions were rated before the experiment with a mean of -0.6 (s.d. = 1.4) and after the experiment with a mean of −0.5 (s.d. = 1.7). Juice ratings were significantly higher than ion water ratings ($F_{1,17}$ = 126.5, $p < 0.001$) and there was no main effect of time (before/after experiment) and no interaction between liquid (juice/ion water) and time. Participants’ most preferred juice was used as their “reward” and their most neutrally rated ion water was used as their “non-reward”.

2.5. Main experiment

Participants completed a random dot-motion discrimination task with the following sequence of events in each trial (Fig. 1). First, a red fixation point was presented in the center of the black screen for 1 s. Second, a cloud of small white dots appeared around the red fixation point and these had a global motion direction of leftwards or rightwards for 0.5 s (speed = 5 deg/s, density = 16.7 dots/deg, size of a dot = 0.10×0.07 deg^2, visual angle = 10°). Each small white dot was shown on a given video frame, and then shown three frames later, either displaced to the left or right (to indicate global motion while preventing the participants from following any one dot with their eyes) or at a random location. Then, the dots disappeared leaving only the red fixation point onscreen for 4 s. The participants were able to respond their perceived dot-motion direction at any point from the onset of the white cloud of dots until the offset of this red fixation point; in total this made a 4.5 s response window. The participants were instructed to press the button in their left hand if they perceive the dots as moving leftward, and vice versa. In reality, the dots moved leftwards in half of the trials and rightwards in the other half (order determined using Optseq2 (Greve, 2002)). When the participants responded, the fixation point changed to a darker red. Subsequently, participants were provided with either 5 ml of juice or 5 ml of ion water, which took 2 s to be delivered via polythene tubes which were hooked up to a Multi-Phaser syringe pump system (New Era Pump Systems Inc.). The fixation point then changed its size and turned green for 0.5 s to indicate that the liquid could be swallowed. Participants were told not to swallow the

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