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Medial frontal cortex response to unexpected motivationally salient outcomes☆

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ABSTRACT

The medial frontal cortex (MFC) plays a central role allocating resources to process salient information, in part by responding to prediction errors. While there is some recent debate, the feedback-related negativity (FRN) is thought to index a reward prediction error by signaling outcomes that are worse than expected. A recent study utilizing electric shock provided data inconsistent with these accounts and reported that the omission of both appetitive (money) and aversive outcomes (electric shocks) elicited a medial frontal negativity. These data suggest that the ERPs within this time range support a salience prediction error that responds to unexpected events regardless of valence. To compare the reward and salience prediction error models, we employed a design that delivered both appetitive (monetary) and aversive (noise burst) outcomes. Participants completed a passive S1/S2 prediction design where S1 predicted S2 with 80% accuracy and S2 predicted the outcome with 100% accuracy. We compared both earlier and later ERP responses over the medial frontal cortex to compare the salience and reward prediction hypotheses. Considering both time windows, the ERP response to S2 in the early time window was most positive when S2 signaled that an outcome was unexpectedly delivered and in the later time window, was most negative when an outcome was unexpectedly withheld, regardless of outcome valence. Thus, these results are more consistent with a salience prediction error rather than a reward prediction error.

1. Introduction

The medial frontal cortex (MFC) is implicated in a wide variety of cognitive control functions: calculating prediction errors (Knutson and Cooper, 2005), coding response conflict (Carter et al., 1998), error monitoring (Gehring et al., 1993), and evaluating action-outcome contingencies (Rushworth and Behrens, 2008). The anterior cingulate cortex (ACC), a region within MFC, is thought to integrate information about task-relevant events and rewarding outcomes in order to select actions that yield optimal value, a necessary step for successful decision-making (Ridderinkhof et al., 2004; Rushworth and Behrens, 2008). One way the brain selects appropriate actions is to calculate reward prediction errors (RPEs) or the difference between expected outcomes and delivered outcomes (Schultz et al., 1997; Sutton and Barto, 1998).

Scalp event-related potential (ERP) recordings originally identified medial frontal negativities thought to represent this RPE: an error-related negativity (ERN) generated to behavioral errors and a feedback-related negativity (FRN) generated by negative feedback or punishing outcomes (Dehaene et al., 1994; Gehring and Willoughby, 2002; Miltner et al., 1997; Scheffers et al., 1996; Yeung et al., 2004). Holroyd and Coles (2002) suggested that these components represent a RPE signal from the ventral tegmental area (VTA) to the ACC, signaling when an outcome is worse than expected. VTA dopamine neurons increase firing to unexpected rewards and suppress firing to unexpected withheld rewards, providing a valence-sensitive signal to better or worse than expected outcomes (Schultz et al., 1997).

While the FRN was initially defined by the difference wave between positive and negative outcomes, it has been debated which condition (the positive or negative feedback) drives this difference (Holroyd and Krigolson, 2007; Holroyd et al., 2008). For instance, the negativity to losses in gambling tasks resembles the N200 component, which occurs in response to unexpected task-relevant stimuli signaling the need for cognitive control (Folstein and Van Petten, 2008; Holroyd, 2004). Subsequent studies argue that this medial frontal negativity is a baseline N200 response that occurs to all unexpected events and is suppressed by another overlapping component occurring to surprising rewards (Reward Positivity: RewP) in a similar time range (Baker and Holroyd, 2008; Holroyd et al., 2008; Proudfit, 2015). The RewP and N200 are suspected to have different neural generators and time-frequency characteristics. The N200 has a suggested neural generator in

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the ACC and reflects theta-band activity signaling the need for cognitive control, while the RewP is thought to reflect basal ganglia influenced delta-band activity signaling reward prediction errors (Bernat et al., 2011; Cavanagh, 2015; Foti et al., 2015). Notably, a neural generator in the basal ganglia is controversial as current ERP technology is unlikely to detect current from non-pyramidal cells within the striatum (Cohen et al., 2011) and others have localized this signal to cortical structures such as the ACC (e.g., Nieuwenhuis et al., 2005). While the source of the RewP is debated, it is likely that dopamine plays some role in the generation of the component (Mueller et al., 2014; Santesso et al., 2009). Additionally, one study conceptualized the RewP (elicited in response to unexpected rewards) as an anterior positivity (P2a), which occurs during attention selection and is thought to represent the identification of task-relevant stimuli by the dopamine reward system (Potts et al., 2006). Subsequently, Soder et al. (2016) determined that the RewP and P2a had overlapping spatial and temporal characteristics, suggesting they may represent the same component. However, another study employing PCA suggested that the RewP peaks in between the frontal P2 and slow wave components, separating it from the other positive anterior waveforms (Foti et al., 2011). Therefore, the distinction between the P2a and the RewP is not well defined.

Although a number of studies and a major meta-analysis suggest that the RewP/FRN reflects a RPE (Sambrook and Goslin, 2015), competing accounts suggest that these components might instead conform to a salience prediction error (SPE; Oliveira et al., 2007; Pearce and Hall, 1980). One possible explanation is that we typically observe a larger negativity to losses because negative outcomes are more salient than positive outcomes (Oliveira et al., 2007). Supporting an SPE model, several studies reported medial frontal negative ERPs in response to unexpected events, regardless of valence (Ferdinand et al., 2012; Garofalo et al., 2014; Hauser et al., 2014; Huang and Yu, 2014; Pfabigan et al., 2015; Sallet et al., 2013; Talmi et al., 2013). These results are consistent with recent evidence that a collection of dopamine neurons may also respond to unexpected punishing outcomes in addition to rewarding outcomes (Matsumoto and Hikosaka, 2009). An alternative explanation is that the negativity reported in these studies represents the conflict N200 as proposed by the N200/RewP hypothesis. While it is unclear why an overlapping RewP was not observed in these studies, one possibility is that these data represent a shift in the time course of the RewP.

Notably, most studies have employed either monetary wins/losses or positive/negative performance feedback. While monetary loss is considered a negative outcome in valence, it represents the non-occurrence of an appetitive outcome (i.e., loss of money). On the other hand, outcomes such as electric shock or loud noise bursts represent the occurrence of an aversive outcome. Of the few studies that have examined the effect of aversive stimuli on the FRN, results have been mixed. Talmi et al. (2013) were the first group to measure the FRN response to non-monetary punishing-predictive stimuli (aversive shocks) and they observed a negativity in the FRN time range when an outcome (either aversive or appetitive) was expected but then later not delivered. On the other hand, a positivity in the same time range occurred when no outcome (again regardless of valence) was expected and later delivered. These results indicate that the neural system(s) indexed by the RewP/FRN may respond in a polarized manner to violations of salience prediction (rather than reward prediction), producing a positive ERP deflection to the unexpected presence and a negative deflection to the unexpected absence of a salient stimulus regardless of valence. Garofalo et al. (2014) similarly reported larger negativities when a salient (aversive shock) outcome was delivered at a delayed time compared to an anticipated time. The same effect was not found for neutral outcomes, indicating that the negativity was not just the unexpected absence of a stimulus, but was specific to a motivationally salient stimulus. Heydari and Holroyd (2016) and Mulligan and Hajcak (this issue) both had participants complete tasks with rewarding (money) and punishing (shock) condition and described opposing results. Heydari and Holroyd (2016) reported a typical RewP response in the rewarding condition to unexpected monetary outcomes but a delayed RewP in the punishing condition to the omission of an imminent punishment, suggesting the RewP does not represent a salience effect. It remains unclear why the RewP would be delayed in the punishing condition and contradictory to this account, Mulligan and Hajcak (this issue) reported that the RewP actually occurred earlier in the punishment condition compared to the reward condition.

While inconsistent with the RPE model of the RewP/FRN, the results of Talmi et al. (2013) support another theory of MFC function: the Predicted Response Outcome (PRO) model (Alexander and Brown, 2011). The PRO model proposes that the MFC is responsible for predicting action-outcome contingencies and updating these predictions if something unexpected occurs. Neurons in the MFC are inhibited when an expected outcome is delivered, but excited when an outcome that is expected is withheld, in turn updating the current outcome predictions. As such, the PRO model proposes that MFC responds to the unexpected “non-occurrence” of an important stimulus (e.g., a monetary reward or an aversive shock; Alexander and Brown, 2011). EEG, fMRI, and single cell studies that reported MFC activation to surprising events support the PRO model (Garofalo et al., 2014; Matsumoto et al., 2007; Talmi et al., 2013; Wessel et al., 2012).

While the results of Talmi et al. (2013) have important implications for the RewP, the study design included 16 conditions, which may have introduced noise into the results. Heydari and Holroyd (2016) employed an active RewP task with only 4 conditions, where participants had to navigate a T-Maze that either lead to a reward (money) or no reward (no money) and punishment (shock) or no punishment (no shock). Additionally, Heydari and Holroyd (2016) argued that the effects of the RewP are larger when the participants feel a sense of control over the outcomes in a task (Sambrook and Goslin, 2015). However, while the PRO model is specifically action based, both appetitive (Potts et al., 2006) and aversive (Talmi et al., 2013) prediction errors have been observed in passive tasks.

As Heydari and Holroyd (2016) employed a behavioral task with 4 possible conditions and Talmi et al. (2013) employed a passive task with 16 possible conditions, it is unclear what influenced the differing results. The current study utilized a more simplified passive design comparable to Talmi et al. (2013) with just 8 conditions instead of 16 to test whether results were consistent with the RPE or SPE models. We employed a task that has reliably elicited results consistent with a polarized RPE within the appetitive domain (Franken et al., 2010; Potts et al., 2006) with an additional aversive domain condition. Possible outcomes included unexpected/expected and delivered/withheld outcomes (either money or loud noise bursts). If the unexpected absence of aversive stimuli elicits a positivity (RewP overtop the N200) and the unexpected presence of aversive stimuli elicits a negativity (N200), data would support the RPE model. Alternatively, if the unexpected absence of aversive stimuli elicits a negativity and the unexpected presence of aversive stimuli elicits a positivity, results would be consistent with an SPE model.

2. Materials and methods

2.1. Participants

58 undergraduate participants were recruited via the University of South Florida Department of Psychology subject pool. Eligible participants were English-speaking who reported intact hearing and no hearing correction device, no current treatment or hospitalization for psychiatric disorders, and no reported psychotropic drug use. 2 participants were excluded due to excessive EEG artifact, while 6 others were excluded due to unsuccessful manipulation (i.e., they rated the white noise burst as ‘pleasant’ on a stimulus validation check), leaving 50 participants in the final sample. The sample was 78% female with an average age of 20.94 (*SD* = 4.7). Compensation for assessment