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It's all about timing: An electrophysiological examination of feedback-based learning with immediate and delayed feedback

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ABSTRACT

Feedback regarding an individual's action can occur immediately or with a temporal delay. Processing of feedback that varies in its delivery time is proposed to engage different brain mechanisms. *f*MRI data implicate the striatum in the processing of immediate feedback, and the medial temporal lobe (MTL) in the processing of delayed feedback. The present study offers an electrophysiological examination of feedback processing in the context of timing, by studying the effects of feedback timing on the feedback-related negativity (FRN), a product of the midbrain dopamine system, and elucidating whether the N170 ERP component could capture MTL activation associated with the processing of delayed feedback. Participants completed a word-object paired association learning task; they received feedback 500 ms (immediate feedback condition) following a button press during the learning of two sets of 14 items, and at a delay of 6500 ms (delayed feedback condition) during the learning of the other two sets. The results indicated that while learning outcomes did not differ under the two timing conditions, Event Related Potential (ERPs) pointed to differential activation of the examined ERP components. FRN amplitude was found to be larger following the immediate feedback condition when compared with the delayed feedback condition, and sensitive to valence and learning only under the immediate feedback condition. Additionally, the amplitude of the N170 was found larger following the delayed feedback condition when compared with the immediate feedback condition. Taken together, the findings of the present study support the contention that the processing of delayed feedback involves a shift away from midbrain dopamine activation to the recruitment of the MTL.

1. Introduction

Learning is guided by the ongoing evaluation of outcomes, leading learners to preserve, modify, or eliminate specific behaviors, goals, and strategies. This evaluative process is triggered by internal monitoring and by the processing of external feedback. In everyday life, feedback can be delivered immediately or with a delay of seconds to days after an individual's actions. There is a growing body of evidence suggesting that separate neural circuitries operate when the temporal proximity of feedback to the initial action varies. Whereas the processing of immediate feedback is known to recruit the mesocorticolimbic reward system (Bellebaum and Daum, 2008; Holroyd et al., 2004; Gehring and Willoughby, 2002; Holroyd and Coles, 2002; Dehaene et al., 1994), the processing of delayed feedback implicates the medial temporal lobe (MTL) (Foerde and Shohamy, 2011; Foerde et al., 2013). More specifically, the anterior cingulate cortex (ACC) has been found to be activated in the context of feedback processing and performance monitoring (e.g., Carter et al., 1998; Critchley et al., 2005; Mies et al., 2011; Rodriguez, 2009), and identified as a likely generator of the feedback-related negativity (FRN) (e.g Nieuwenhuis et al., 2004), a component of the event-related potential (ERP) that is elicited by feedback in probabilistic and declarative learning tasks. A dramatic performance impairment on a probabilistic learning task with delayed feedback as compared with immediate feedback among people with disorders involving the MTL (Foerde et al., 2013), and evidence of MTL cortices activation by delayed but not immediate feedback in such tasks (e.g., Foerde and Shohamy, 2011), support the notion that the MTL is necessary to process delayed feedback. By contrast, although most FRN studies have involved relatively immediate feedback, a few studies have revealed that FRN amplitude is smaller for longer delays (Peterburs et al., 2016; Weinberg et al., 2012; Weismuller and Bellebaum, 2016), which supports the contention that this system is not optimal for processing feedback after longer delays. These considerations suggest that the MTL may compensate for feedback processing at longer delays,

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but it remains to be determined whether the increased MTL activation associated with delayed feedback is captured by scalp recording. The present study aimed at examining the known feedback related ERPs in relation to immediate and delayed feedback in a feedback-based declarative learning task, and at exploring a candidate ERP that may capture MTL activation associated with delayed feedback.

1.1. Feedback related negativity (FRN) and frontocentral positivity (FCP) as electrophysiological markers of feedback processing

The reinforcement learning (R-L) theory posits that outcomes of ongoing events are constantly evaluated, resulting in a phasic increase or decrease in dopaminergic signals that are communicated to the basal ganglia and the frontal cortex (Berger et al., 1991; Holroyd and Coles, 2002). The phasic decrease and increase of dopaminergic input (Montague et al., 1996) that allows for the evaluation of outcomes led researchers to suggest that the mesencephalic dopamine system can support learning with strict timing requirements, such that feedback is more effective when it coincides with the activity of pre- and postsynaptic processes (Wickens et al., 1996). In other words, this learning system may be most efficient when feedback is immediate and occurs with close temporal proximity to the initial action or response (Dobryakova and Tricomi, 2013). The feedback related negativity (FRN) ERP has been proposed to be a product of the reinforcement learning system. This ERP component has a fronto-central scalp distribution and a maximal peak about 250–300 ms after the presentation of feedback (Miltner et al., 1997). According to the R-L theory, the FRN is generated by the disinhibition of neurons in the anterior cingulate cortex caused by a phasic decrease in dopaminergic input when outcomes are worse than expected (Holroyd and Coles, 2002). A recent update to this proposal holds that the difference in the ERP waveforms to positive and negative feedback is mainly driven by increased inhibition of ACC following positive feedback (Holroyd et al., 2008; see Proudfit, 2015 for review). A large body of evidence localizing the generation of the FRN to the anterior cingulate cortex (ACC) (Bellebaum and Daum, 2008; Carter et al., 1998; Critchley et al., 2005; Dehaene et al., 1994; Holroyd et al., 2004; Gehring and Willoughby, 2002; Holroyd and Coles, 2002) lends support to the reinforcement learning theory of the FRN, and to the suggestion that the FRN is generated by a system suited for the processing of immediate feedback.

The FRN is followed by a frontocentral positivity (FCP) with a latency range of 200–400 ms following the presentation of negative feedback (Arbel et al., 2013; termed P3a by Butterfield and Mangels, 2003). The FCP has been found sensitive to valence and learning outcomes (Arbel et al., 2013). While the neural substrate responsible for producing this fronto-central component has not been identified, it's possible function has been conceptualized as the product of an orienting attentional process (Butterfield and Mangels, 2003), that is sensitive to feedback processing but is not necessarily unique to the processing of feedback.

1.1.1. FRN and delayed feedback

Several studies are available to date that investigated the effect of delayed feedback on the FRN. Weinberg et al. (2012) presented participants with loss and gain feedback with short (1 s) and long (6 s) delays within the context of a gambling task. They reported that the FRN elicited by negative feedback under the short delay condition showed a larger negativity when compared with the long delay condition. Peterburs et al. (2016) compared the effect of increasingly longer delays on the FRN amplitude during a probabilistic learning task. Participants were tasked with learning stimulus-response-outcome associations. Feedback was presented with a short delay (500 ms), medium delay (3500 ms), or a long delay (6500). Analysis of the difference waves indicated a decrease in amplitude with increasing time delay, with the largest FRN difference wave in the short delay condition, and the smallest FRN difference wave in the long delay. However, a peak-to-peak measure of the FRN, defined as the difference between the largest negative peak of the FRN and the positivity preceding it, demonstrated that long delays were associated with the largest FRN magnitude, when compared with short delays. It is important to note that the difference wave measure included in its time window (250–400 ms) a portion of the proceeding fronto-central positivity (FCP). The peak-to-peak measure, on the other hand, subtracted the largest negativity from the preceding P2. Both the preceding P2 and the proceeding FCP could have added to the variance in the data and contributed to the contrasting results under the two methods of measurement. Weismuller and Bellebaum (2016) employed a probabilistic learning task with feedback presented after 500 ms (termed immediate) and with a delay of 6500 ms, to evaluate whether FRN elicited by delayed feedback is sensitive to expectancy. A difference wave analysis resulted in reduced FRN amplitude for delayed feedback, but similar sensitivity of FRN elicited by immediate and delayed feedback to expectancy. Taken together, very few studies have investigated the FRN sensitivity to the timing of feedback, and the results point to processing differences between immediate/short delayed and long delayed feedback. While the FRN to delayed feedback was examined in the context of gambling and probabilistic tasks, it has yet to be evaluated in a declarative learning task, in which feedback guides the learner throughout the learning process. Such task may be suitable for exploring the interaction between the MTL which is recruited for binding information to create and store correct associations, and the mesencephalic dopamine system that is involved in reinforcement learning.

1.2. The involvement of the MTL in processing delayed feedback

When reinforcement is delayed, fundamental changes are observed in the responses of dopaminergic neurons of the reward processing system (Fiorillo et al., 2008; Kobayashi and Shultz, 2008). Delays of even a few seconds have been shown to disrupt the activity from the ventral tegmental area to the striatum (Foerde and Shohamy, 2011; Maddox et al., 2003). Moreover, rewards that are predicted but are presented with a delay of several seconds produce a signal similar to that of an unpredicted reward (Fiorillo et al., 2008). Therefore, the mesencephalic-striatal system may be limited to immediate feedback conditions, and may not be well suited for learning from delayed feedback (Foerde and Shohamy, 2011). In learning conditions involving delayed feedback, the MTL may play a major role. The MTL, which consists of the hippocampus and the surrounding perirhinal, entorhinal, and parahippocampal cortices is essential for long term declarative, episodic memory. More specifically, bilateral anterior medial temporal lobe (MTL) regions have been implicated in forming contextual associations, and in binding multiple elements of an experience (Aminoff et al., 2013; Cohen and Eichenbaum, 1993; Jackson and Schacter, 2004; Mitchell et al., 2000; Schacter and Wagner, 1999). Evidence exists that midbrain dopamine neurons, which project directly to the hippocampus and to the surrounding MTL cortices (Samson et al., 1990; Gasbarri et al., 1994), contribute to successful binding between experiences separated by time (Cohen and Eichenbaum, 1993; Shohamy and Wagner, 2008). Such binding, mediated by tonic dopamine signals (Niv et al., 2007), begins before the experiences and continues into a temporal window of hours or days (Shohamy and Adcock, 2010). Foerde and Shohamy (2011), in an *f*MRI study of healthy young adults performing a probabilistic learning task, demonstrated the recruitment of the striatum during learning with immediate feedback, and increased activation of the hippocampus with delayed feedback. Data from the same authors showed that individuals with Parkinson's disease, whose striatum is known to be degraded, were impaired in learning from immediate but not delayed feedback (Foerde and Shohamy, 2011). Conversely, individuals with MTL damage exhibited impaired learning with delayed but not immediate feedback

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