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Auditory event-related potentials over medial frontal electrodes express both negative and positive prediction errors

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ABSTRACT

While the neuronal activation in the medial frontal cortex is thought to reflect higher-order evaluation processes of reward prediction errors when a reward deviates from our expectation, there is increasing evidence that the medial frontal activity might express prediction errors in general. However, given that several studies examined the medial frontal event-related potentials (ERPs) by comparing signals triggered by different stimuli and different anticipations, it remains an open question whether the medial frontal signals are sensitive to the valence of prediction errors. Here we orthogonally manipulated expectation magnitude (i.e., large/small expectation) and expectation confirmation (i.e., fulfilled/violated expectation) in a target detection task with rewards. We found that the medial frontal ERPs were more negative-going for unexpected outcomes in comparison with expected outcomes, regardless of whether a large/small reward was expected. The result supports the idea that the medial frontal signals express prediction errors in general regardless of their valence.

1. Introduction

Motivated actions are believed to be guided by reward prediction errors, which are engendered when a reward deviates from our expectation. It was postulated that reward prediction errors are derived from dopaminergic projections from the ventral tegmental area to the medial frontal cortex, most likely to the anterior cingulate cortex (ACC) (Holroyd & Coles, 2002; see Walsh & Anderson, 2012 for a review). Importantly, dopamine neurons in the ventral tegmental area were reported to show suppressed firing when predicted reward is omitted and enhanced firing when unpredicted reward is delivered (Schultz, 1997).

Event-related potentials (ERPs) associated with such process include the medial frontal P2 and the feedback-related negativity (FRN). The two signals are believed to reflect the same evaluation function (Potts, Martin, Burton, & Montague, 2006), since they share similar spatiotemporal distributions and response patterns. Specifically, these medial frontal signals peaking at around 250–350 ms after stimulus onset were reported to be consistent with the activity of midbrain dopamine neurons, being more negative-going to the omission of predicted reward and more positive-going to the delivery of unpredicted reward (Martin, Potts, Burton, & Montague, 2009). Moreover, these medial frontal signals were found to be more negative-going for losses and more positive-going for gains (Gehring & Willoughby, 2002; Holroyd, Larsen, & Cohen, 2004). It is, thus, suggested that the medial frontal ERPs in question carry information about the valence (i.e., negative/positive value) of the prediction errors.

However, other ERP research called this suggestion into question. For example, it was shown that, when participants receive unexpected feedback concerning their performance, the medial frontal signals are more negative-going not only for unexpected negative feedback but also for unexpected positive feedback (Oliveira, McDonald, & Goodman, 2007). The notion of valence-independent medial frontal signals is further supported by research where the feedback was not related to participants' performance. For example, Talmi, Atkinson, and El-Deredy (2013) showed that the medial frontal signals are more negative-going for both reward and pain omission in comparison with reward and pain delivery. Garofalo, Maier, and di Pellegrino (2014) further demonstrated that the stronger the outcome-delivery expectancy, the stronger

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the negative-going medial frontal signals for the unexpected outcomes. In another study where participants were presented with monetary gain/loss feedback, Huang and Yu (2014) found that the medial frontal signals are more negative-going for both gain and loss omission in comparison with gain and loss delivery. All these findings suggest that the medial frontal signals reflect prediction errors regardless of their valence; that is, they are more negative-going not because a desirable outcome is missing but because a predicted outcome is missing.

Is the presence/absence of the valence effect related to whether or not the feedbacks are used to improve performance? Holroyd, Krigolson, Baker, Lee, and Gibson (2009) proposed that the expectation effect on the medial frontal ERPs was the largest when feedbacks can be used to optimise behaviours. Given that the medial frontal signals are sensitive to subjective expectations (Ferdinand, Mecklinger, Kray, & Gehring, 2012; Hajcak, Moser, Holroyd, & Simons, 2007), it is possible that the valence effect appears when feedbacks are informative (i.e., when the expectation effect is large) and disappears when feedbacks are not informative (i.e., when the expectation effect is not as large). However, valence-dependent expectation effect was already found with both active paradigms (Gehring & Willoughby, 2002; Holroyd et al., 2004) and passive paradigms (Martin et al., 2009; Potts et al., 2006). On the other hand, valence-independent expectation effect was documented in studies where feedbacks were either dependent (Oliveira et al., 2007) or independent (Huang & Yu, 2014; Talmi et al., 2013) of one's behavioural responses. Therefore, this explanation seems unlikely.

Is it possible that the discrepancy in the literature is due to different measures of the medial frontal ERPs? For example, analysing one frontocentral electrode, Ferdinand et al. (2012) found the valence effect with a mean amplitude measure but not with a peak-to-peak measure. However, there does not seem to be a systematic correspondence between the measures and the findings in the literature. Specifically, the measures adopted in studies supporting the valence-dependent account include the mean amplitude measure over multiple frontal electrodes (Gehring & Willoughby, 2002; Martin et al., 2009; Potts et al., 2006) and the base-to-peak measure on one frontocentral electrode (Holroyd et al., 2004). Similarly, the measures adopted in studies supporting the valence-independent account include the mean amplitude measure on one frontal electrode (Huang & Yu, 2014) and the base-to-peak measure over three frontocentral electrodes (Oliveira et al., 2007), as well as the cluster maxima measure (Talmi et al., 2013). Therefore, this alternative also seems unlikely.

Since evidence in the literature concerning the question of whether or not the medial frontal signals are valence-sensitive is contradictory, the issue deserves systematic investigation. It is to be noted that, in some of the previous studies reporting valence-dependency of the medial frontal ERPs, negative and positive prediction errors were signalled by different stimuli (e.g., a picture of a lemon and a picture of a gold bar in the studies of Potts et al. (2006) and Martin et al. (2009)). ERPs triggered by these stimuli are not necessarily comparable, the more so as it was reported that the medial frontal signals can be affected by the perceptual characteristics of the outcome stimuli (Liu & Gehring, 2009). Therefore, it is possible that the valence-dependent effects reported in these studies reflect, entirely or to some extent, bottom-up effects driven by these differences. On the other hand, several studies reporting valence-independent medial frontal ERPs varied the valence of prediction errors by introducing differences in what had been predicted in the first place (i.e., appetitive and aversive outcomes, respectively) (Huang & Yu, 2014; Talmi et al., 2013). Moreover, they used a procedure where there is a cue signalling how likely the expected appetitive and aversive outcome was to be omitted. The medial frontal ERPs were time-locked to the cue, not the outcome. The ERPs to the cue, therefore, might involve certain preparatory processes for the outcome. This makes it difficult to determine whether the valence-independent medial frontal ERPs observed here simply reflect some common preparatory processes rather than prediction errors.

Overall, although each of the aforementioned studies gives valuable insight into the question at hand, the procedural differences between previous studies make it very difficult to understand the contradictory results. Given these contradictions, it is necessary to revisit the question at hand and comprehend the influences of various experimental approaches on medial frontal ERPs. We designed a new experimental procedure that is meant to allow for the most basic comparison of negative and positive prediction errors to figure as a starting point for further systematic investigation. To be precise, we created a paradigm in which stimuli are strictly counterbalanced across conditions and in which rewards are always anticipated while the outcome instantaneously signals whether the expectation is fulfilled/violated. Also, the feedback cannot be used to improve one's behaviour. More specifically, we orthogonally manipulated expectation magnitude (i.e., large/small expectation) and expectation confirmation (i.e., fulfilled/violated expectation) in a target detection task. Here, a large expectation violated by the presentation of a small outcome would create negative prediction errors (because the outcome is worse than expected) and a small expectation violated by the presentation of a large outcome would create positive prediction errors (because the outcome is better than expected). Participants were instructed to press a key to a target as soon as possible to gain a reward while their electroencephalography (EEG) was recorded. If the medial frontal signals are sensitive to the valence of prediction errors, negative and positive prediction errors should be associated with different medial frontal signals. If valence is not crucial, as recent insights on the role of dopamine suggested (Matsumoto & Hikosaka, 2009; Metereau & Dreher, 2013), negative and positive prediction errors should be represented in similar manner. We found that both negative and positive violations of expectation were associated with more negative-going medial frontal ERPs. The result supports the idea that the medial frontal signals express prediction errors in general regardless of their valence.

2. Materials and methods

2.1. Participants

Sixteen healthy volunteers (average age 28; four males; all right-handed) with no history of neurological, psychiatric, or visual/hearing impairments as indicated by self-report participated in the experiment. Participants gave written informed consent and were paid for participation by hour plus an additional reward between 1 and 7 euros based on the bonus points gained throughout the experiment. Ethical approval was granted by the CPP (Comité de Protection des Personnes) Ile de France II. Two participants were excluded from data analysis as one encountered a technical failure during the EEG recording and one failed to provide correct answers to more than 50% of the catch trials, leaving fourteen participants in the final sample (average age 28; three males; all right-handed).

2.2. Stimuli

The targets were one smiling face and one frowning face, presented in grey against a black background. The rewards were signalled by two sinusoidal tones (high pitch tone: 3136 Hz; low pitch tone: 392 Hz) with the loudness of 80 phons (i.e., 80 dB for tones of 1000 Hz) and the duration of 50 ms (including 5 ms rise/fall times) generated in Matlab, presented binaurally via headphones (Sennheiser PX200).

2.3. Procedures

A total of 10 blocks of 93 trials were presented. A trial started with the presentation of a target (i.e., either a smiling face or a frowning face) for up to 400 ms. Participants were explicitly told that the smiling face and the frowning face were associated with different reward expectancies as follows. The smiling face meant that there was an 80% chance of getting a large reward (i.e., 9 bonus points) and a 20% chance of getting a small reward (i.e., 1 bonus point). The frowning face meant that there was an 80% chance of getting a small reward (i.e., 1 bonus point)