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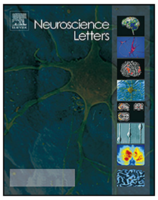

Sensitivity of frontal beta oscillations to reward valence but not probability

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HIGHLIGHTS

- Rewards elicit beta power over frontal areas of the scalp.
- We showed that beta power was mainly sensitive to feedback valence.
- We showed that beta power was not sensitive to feedback probability.
- Beta cannot index a reward prediction error.
- Beta might relate to a different reward processing function.

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ABSTRACT

Reward feedback elicits a brief increase in power in the high-beta frequency range of the human electroencephalogram (EEG) over frontal areas of the scalp, but the functional role of this oscillatory activity remains unclear. An observed sensitivity to reward expectation (HajiHosseini, Rodríguez-Fornells, and Marco-Pallarés, 2012; [2]) suggests that reward-related beta may index a reward prediction error (RPE) signal for reinforcement learning. To investigate this possibility we reanalyzed EEG data from two prior experiments that revealed RPEs in the human event-related brain potential (Holroyd and Krigolson, 2007 [12]; Holroydet al., 2008 [13]). We found that feedback stimuli that indicated reward, when compared to feedback stimuli that indicated no-reward, elicited relatively more beta power (20–30 Hz) over a frontal area of the scalp. However, beta power was not sensitive to feedback probability. These results indicate that reward-related beta does not index an RPE but rather relates to a different reward processing function.

1. Introduction

Several studies have reported that presentation of reward-related feedback stimuli enhances power in the high-beta frequency range (∼20–35 Hz) of the human electroencephalogram (EEG) [1–3] and magnetoencephalogram [4] over frontal areas of the scalp. Although recent proposals have suggested that reward-related beta[1] activity might reflect coupling between neurocognitive processes involved in motivation, attention, and memory [5], or neural synchronization that facilitates learning from feedback [6], there is a paucity of data addressing this question. Of note, in one recent study unexpected gains in a gambling paradigm elicited relatively more beta power compared to expected gains [2]. This sensitivity of beta power to reward expectancy suggests that beta oscillations might index a reward prediction error (RPE), an important training signal in computational theories of reinforcement learning that indicates whether ongoing events are “better” or “worse” than expected [7,8]. Consistent with this possibility, substantial evidence indicates that RPEs are carried by the midbrain dopamine system to their neural targets [9] including frontal areas of cortex [10].

A neural signal that encodes an RPE must be sensitive to a specific interaction between the valence and probability of the eliciting outcome [11]. If beta reflected an RPE signal, then we would expect relatively more beta following unexpected rewards compared to expected rewards, and relatively less beta following unexpected errors compared to expected errors. To investigate whether beta has these properties, we reanalyzed data from two previous EEG experiments that revealed an RPE signal in the human event-related brain potential (ERP) [12,13]. In these experiments, subjects

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[1] For conciseness, hereafter we use “beta” to refer to oscillatory activity in high-beta frequency range (20–35 Hz).

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engaged in a time-estimation task in which the correct (rewarded) and incorrect (not rewarded) responses occurred with high or low probability, as determined by a staircase procedure that adjusted task difficulty from trial to trial (see Method). We reasoned that if reward-related beta reflects an RPE signal, then that property should be observed in a task already known to elicit an RPE signal in the ERP.

2. Method

EEG datasets were reanalyzed from two previous studies: dataset 1 (D1) from Holroyd and Krigolson [12] and dataset 2 (D2) from Holroyd and colleagues [13]. In both studies the EEG was recorded from participants while they performed a time-estimation task. Because the studies were carried out using nearly identical protocols, the data were reanalysed together (with dataset as a between-subject factor) to increase statistical power.

2.1. Participants

D1 and D2 included the data of seventeen (8 male and 9 female; 19.6 ± 2.8 years old) and twelve (6 male and 6 female; 26.7 ± 10.5 years old) participants, respectively, who were undergraduate students at the University of Victoria receiving extra course credits for their participation, or who were paid volunteers. The studies were conducted in accordance with the ethical standards prescribed in the Declaration of Helsinki and were approved by the human subjects review board at the University of Victoria. Informed written consent was obtained from all participants prior to the experiment. The data of two of the participants associated with D1 were eliminated from the analysis because of an insufficient number of trials following artifact rejection. Therefore we analyzed the data of a total of twenty-seven participants across both datasets.

2.2. Task

In both studies, on each trial participants were required to press a left mouse button when they estimated that 1 s had elapsed following presentation of an auditory cue. At the end of each trial, a visual feedback stimulus indicated whether the response was correct or incorrect. The feedback stimuli consisted of a white plus sign and a white zero(3°, 1000 ms) presented on a high contrast black background. The response was initially evaluated as correct if it was produced within a time window spanning 900–1100 ms following cue onset, and was evaluated as incorrect otherwise. The width of the time window varied from trial to trial by condition according to the following staircase procedure. In the *control* condition, the window size increased by 10 ms following every error response and decreased by 10 ms following every correct response. In the *probable error* condition, the window size increased by 3 ms after every error response and decreased by 12 ms after every correct response, and in the *probable correct* condition, the window size increased by 12 ms after every error response and decreased by 3 ms after every correct response. This staircase procedure equated the probability that participants would receive correct or error feedback across conditions (about 75% error feedback in the probable error condition and 75% correct feedback in the probable correct condition). Participants in D1 completed six blocks of 75 trials: two in the control, two in the probable error, and two in the probable correct conditions. Participants in D2 did five blocks of 100 trials: one in the control, two in the probable error, and two in the probable correct conditions. Participants were told at the start of the experiment that some conditions would be harder than others. Because the order of the control condition was not counterbalanced with the other conditions in either study (the control condition always occurred first), our reanalysis included only trials associated with the probable correct and probable error conditions (300 trials in D1 and 400 trials in D2). Note that the order of the probable correct and probable error conditions was counterbalanced across subjects for both datasets. In D2, reward and error feedback stimuli also indicated 3-cent and 0-cent monetary outcomes but in D1, they were not associated with monetary outcomes. For a complete description of the task, please refer to Holroyd and Krigolson [12].

2.3. Data acquisition

The EEG was recorded from 41 electrode locations in D1 [12] and 64 electrode locations in D2 [13] using BrainVision Recorder software (Brain Products, Munich, Germany). Electrodes were arranged according to the standard 10–20 layout [14] and were referenced to the average voltage across the channels. The two electrode montages were overlapping but not identical. Vertical and horizontal ocular movements were recorded by an electrode placed under the right eye (re-referenced offline to FP2), and two on the outer canthi of the right and left eyes (re-referenced offline to each other), respectively. Electrode impedances were kept under 10 kΩ. Data were sampled at 250 Hz and band pass filtered by the amplifiers at 0.017–67.5 Hz.

2.4. Data analysis

Data pre-processing was performed in BrainVision Analyzer 2. A band-pass filter (0.1–40 Hz) was applied to the EEG data and epochs of EEG activity were selected from 1 s before to 1 s after the onset of feedback stimuli. Data were subsequently re-referenced to the average value recorded at the mastoids. Ocular correction was performed using the Gratton et al. [15] algorithm as implemented in the Analyzer software. Feedback segments were baseline-corrected by subtracting, for each channel, subject, and electrode, the average voltage values during the 100 ms prior to the feedback stimulus from the subsequent voltages in the epoch. EEG artifacts were identified and rejected according to the following criteria: any abrupt change of voltage greater than 35 μV from one time sample to the next, any difference between the negative and positive peaks in a 200 ms interval that exceeded 150 μV, and any activity that was consistently smaller than 0.5 μV in a 100 ms interval were considered artifacts and the corresponding segment was rejected for all channels. On average, 25% of data were rejected.[2] Topographical scalp maps were plotted with EEGLAB [16].

Data were exported to MATLAB for time-frequency analyses. To extract time-frequency information, a 2 s epoch centered on the feedback presentation time was convoluted with a complex Morlet wavelet:

$$w(t, f_0) = \left(2\pi\sigma_t^2\right)^{\frac{-1}{2}} \exp\left(\frac{-t^2}{2\sigma_t^2}\right) \exp(2\pi i f_0 t) \qquad (1)$$

The wavelet family ratio $\left(\frac{f_0}{\sigma_f}\right)$, where $\sigma_f = \frac{1}{2\pi\sigma_t}$, was set to 6.7 [3] and was linearly scaled based on the frequency range of 1–40 Hz. Time-frequency power was extracted relative to a 100 ms baseline before the feedback on each trial as (trial power-baseline power)/baseline power. Then the power values were averaged separately for each condition and subject. We expected the beta power contrast to occur between 20 Hz and 30 Hz at about 250–500 ms following the feedback stimulus according to previous studies [2,3,17]. Therefore, the grand average time-frequency power maps were inspected according to this a priori assumption [18] and the

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[2] This rejection rate is higher than those reported in the original articles due to application of a higher filter cutoff (40 Hz), which retained high-frequency noise as well as signal.