Neuroscience 333 (2016) 264–276

REPRESENTING THE CONSEQUENCES OF OUR ACTIONS TRIAL BY TRIAL: COMPLEX AND FLEXIBLE ENCODING OF FEEDBACK VALENCE AND MAGNITUDE

ISABEL PADRÓN, [a,b] **JOSÉ FERNÁNDEZ-REY,** [b]
CARLOS ACUÑA [a] **AND JOSE L. PARDO-VAZQUEZ** [a,c*]

[a] *Departamento de Fisiología, Facultad de Medicina and Complejo Hospitalario Universitario (CHUS), Universidad de Santiago de Compostela, Spain*

[b] *Departamento de Psicología Social, Básica y Metodología, Facultad de Psicología, Universidad de Santiago de Compostela, Spain*

[c] *Champalimaud Neuroscience Programme, Champalimaud Centre for the Unknown, Portugal*

Abstract—In the last decades it has been shown that two components of the event-related potentials (ERPs), the feedback-related negativity (FRN) and the P300, reflect the evaluation of the outcomes of a given course of action. Within the reinforcement learning theory, the prevailing interpretation of the relationship between FRN and P300 is the classical "independent coding model". This model proposes that the FRN is only sensitive to feedback valence whereas the P300 is only sensitive to feedback magnitude. However, these predictions have recently been challenged and the question remains unsolved. The goal of the present study is to shed light on the effects of outcome valence and magnitude on the FRN and the feedback-P300. The electroencephalographic (EEG) activity was recorded while participants performed a perceptual discrimination task with two levels of difficulty, in which they could receive large or small rewards and penalties. We used receiver operating characteristics (ROC) analyses, which allowed us to analyze the relationship between the outcomes and EEG on a trial-by-trial basis. The results reveal that both components, which are contingent on feedback presentation, are sensitive to outcome valence. Regarding magnitude, this only affects the feedback P300, and only in conjunction with difficulty. Finally, we found that task difficulty has the opposite effect on these components, both in their latencies and discriminability. Our results suggest that the FRN and the feedback-P300 in fact reflect different performance monitoring processes in a flexible way that depends on the behavioral context.

Key words: perceptual decision-making, performance monitoring, outcome evaluation, event-related potential (ERP), feedback-related negativity (FRN), feedback-P300.

INTRODUCTION

The evaluation of the outcomes of previous choices is fundamental to the ability to adapt future behavior, and thus to learn how to make better decisions. In order to succeed in pursuing their goals, organisms are required to learn the relations between actions and their consequences and to use that information to guide future behavior: positive outcomes (or rewards) increase the frequency and intensity of a behavior while negative outcomes reduce them (Sutton and Barto, 1988; Schultz et al., 1997; Nieuwenhuis et al., 2004a; Cohen et al., 2007; Holroyd and Coles, 2008; Schultz, 2008; Hughes and Yeung, 2011; Ullsperger et al., 2014). Single-cell recordings in behaving monkeys, rodents and other species have shown that mesencephalic dopamine neurons encode reward prediction errors; their firing rates increase after unexpected rewards and decrease for outcomes that are worse than expected [see (Schultz, 2000) for a review]. These neurons do not only care about past events; they also change their responses as a function of previous experience, rendering the mesencephalic dopamine system a good candidate for encoding the neural signals that are used to learn from previous outcomes and adapt future behavior accordingly (Schultz et al., 1997; Schultz, 2000; Dayan and Daw, 2008).

Our understanding of the brain mechanisms involved in performance monitoring in humans has also advanced significantly in recent decades, but many unresolved questions remain (Gehring et al., 2012). Most of the current knowledge in this area has arisen through the recording of electroencephalographic (EEG) activity while participants perform highly controlled behavioral tasks (Falkenstein et al., 1991; Gehring et al., 1993; Dehaene et al., 1994; Miltner et al., 1997; Holroyd and Coles, 2002; Yeung and Sanfey, 2004; Hajcak et al., 2005). Since in real life decisions are often evaluated based on feedback available in the environment, many experimental tasks provide, after each behavioral response, information about the correctness of the choice. This provides the participants with trial-by-trial knowledge about whether their decisions fulfill their expectations and goals. When performance feedback is presented, two EEG event-related waves, or

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*Correspondence to: J. L. Pardo-Vazquez, Center for Research in Molecular Medicine and Chronic Diseases, Universidad de Santiago de Compostela, Av. de Barcelona, s/n, 15782, Santiago de Compostela (A Coruña), Spain.
E-mail addresses: isabel.padron@usc.es (I. Padrón), jose.fernandez.rey@usc.es (J. Fernández-Rey), carlos.acuna.castroviejo@gmail.com (C. Acuña), jose.pardo@usc.es (J. L. Pardo-Vazquez).

Abbreviations: ACC, anterior cingulate cortex; EEG, electroencephalographic; ERPs, event-related potentials; FRN, feedback-related negativity; FT, fixation target; LDT, length discrimination task; RL, reinforcement-learning; ROC, receiver operating characteristics; RTs, reaction times.

http://dx.doi.org/10.1016/j.neuroscience.2016.07.025
0306-4522/

event-related potentials (ERPs) components, have been found to be related to performance monitoring.

The first of these components is the feedback-related negativity (FRN), a fronto-central negative deflection that peaks around 250–300 ms after feedback presentation, and the amplitude of which is typically higher for negative than for positive feedback (Gehring et al., 1993; Miltner et al., 1997; Holroyd and Coles, 2002; Nieuwenhuis et al., 2004a; Heldmann et al., 2008). Although different hypotheses have been proposed for its functional meaning (*e.g.*, error detection, conflict monitoring or emotional reaction), the reinforcement-learning (RL) theory (Holroyd and Coles, 2002) seems to be the most widely accepted (San Martin, 2012). This theory holds that the FRN reflects a reward prediction error signal in the anterior cingulate cortex (ACC) that occurs when the monitoring system detects that the consequences of an action are worse than expected (Holroyd and Coles, 2002).

The second component, the P300, is a positive deflection that peaks around 300–600 ms after feedback stimulus presentation and reaches its maximum at parietal-central electrode sites (Sutton et al., 1965; Duncan-Johnson and Donchin, 1977, 1980; Yeung and Sanfey, 2004; Hajcak et al., 2005; Holroyd et al., 2006; Bellebaum et al., 2010; Zhou et al., 2010). It is involved in a large number of cognitive processes, including attention, working memory and motivation (Squires et al., 1975; Duncan-Johnson and Donchin, 1977; Paller et al., 1987; Polich, 2007). Recent studies using decision and outcome evaluation tasks have suggested that this component reflects the evaluation of the functional and affective significance of the stimuli (Yeung and Sanfey, 2004; Hajcak et al., 2005; Nieuwenhuis et al., 2005a; Yu et al., 2007; Luu et al., 2009; Wu and Zhou, 2009; Pfabigan et al., 2011; Schuermann et al., 2012).

It has been proposed that these components encode different aspects of outcome evaluation. Within the RL-theory, the prevailing interpretation of the relationship between FRN and P300 is the independent coding model (Yeung and Sanfey, 2004), according to which the FRN is sensitive to the valence (good vs. bad) of the outcome but not to its magnitude (large vs. small), whereas the P300 is sensitive to magnitude but is independent from valence (Yeung and Sanfey, 2004; Sato et al., 2005; Yu and Zhou, 2006). Over the last two decades several studies have addressed the way in which these components are modulated by outcome valence and magnitude, yet the issue remains unsolved. To summarize, most studies indicate that the FRN is sensitive to the valence of the outcome while the feedback-P300 is sensitive to its magnitude [see (San Martin, 2012) for a review]. However, others argue against this simplistic interpretation. For example, Goyer et al. (2008) showed that the FRN is sensitive to both feedback valence and reward magnitude, and that it is also affected by a combination of several factors, including valence, magnitude, non-chosen options and the history of wins and losses.

In a recent study we described two ERP components that represent, trial-by-trial, the correctness of current choices (Pardo-Vazquez et al., 2014). We also showed that task difficulty has opposite effects on these components, suggesting a functional differentiation between them. Those components are consistent with the main features of the FRN and the feedback-P300; however, the design of that experiment did not allow us to rule out the effect of the behavioral response and, therefore, we were not able to associate them to the feedback. In the present study we have recorded the EEG while the participants performed a two-alternative forced-choice task in which they had to discriminate the length of two lines. To disentangle the contributions of behavioral response and feedback, we have imposed a delay with different durations (500, 1000 and 1500 ms) between behavioral choice and feedback presentation. Moreover, in order to further understand the functional meaning of both ERP components, we manipulated the magnitude of the feedback along with its valence and the difficulty of the task. Since we were interested in the information conveyed by the EEG activity in each trial, receiver operating characteristic (ROC) analyses were conducted to study the trial-by-trial covariation between the EEG activity and different behavioral variables. This methodology, based on signal detection theory [SDT; (Green and Swets, 1966)], has been applied in the study of other ERP components (Philiastides and Sajda, 2006; Bandt et al., 2009; Philiastides et al., 2010).

EXPERIMENTAL PROCEDURES

Participants

Fifteen undergraduate students (11 females) between 19 and 27 years old ($\text{Mean}_{\text{age}} = 21.2$, $SD = 2.59$), with normal or corrected to normal vision and no history of neurological disorders participated in the study. Each participant received ten euros per session and provided written consent to participate in the study.

General procedure

Participants performed the behavioral task in an isolated room with a one-way mirror with the experimenter's room. The computer screen was placed at 57 cm from their eyes and a chin rest was used to maintain the distance from the screen and to avoid head movements. *Superlab 4.5* (www.cedrus.com) was used to control stimuli presentation and to record the participants' responses and reaction times (RTs).

The experiment comprised two stages. The first one, aimed at estimating the psychometric curves for each participant, included one experimental session of about 90 min during which participants performed 720 trials of the length discrimination task (LDT), distributed in four blocks of 180 trials separated by short breaks. Performance in the first session was then used to select the stimuli set for the second stage. The second stage, in which the EEG activity was recorded, included two experimental sessions. Each session lasted for about 90 min and consisted of two consecutive blocks of 290 trials separated by a short break. Each participant performed at least 1160 trials. Sessions were conducted on consecutive days at approximately the same time of