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A Note on the Oddball N200 and the Feedback ERN

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The oddball N200 and the feedback error-related negativity (feedback ERN) are commonly regarded as two distinct components of the event-related brain potential (ERP). However, morphological similarities between the two ERP components suggest that they may in fact reflect the same phenomenon. This paper explores the ramifications of these two mutually-exclusive possibilities. First, if the oddball N200 and the feedback ERN reflect different phenomena, then empirical methods should be developed to dissociate the two. Second, if the two components reflect the same phenomenon, then a unifying theory should be developed to account for them.

Introduction

The event-related brain potential (ERP) provides a means by which cognitive function can be inferred from the temporal and spatial pattern of fluctuating voltages recorded at the scalp (Coles &

Rugg, 1995). Among the spectrum of ERP components that have provided such insight, several components with negative polarities have been proposed to reflect processes involved in executive control. These components include the response error-related negativity (ERN), which is associated with error commission (Falkenstein, Hohnsbein, Hoormann, & Blanke, 1990; Gehring, Goss, Coles, Meyer, & Donchin, 1993); the correct-related negativity (CRN), which is associated with correct responses (Vidal, Hasbroucq, Grapperon, & Bonnet, 2000); the N200, including the oddball N200 and the no-go N200, which are associated with response conflict (Nieuwenhuis, Yeung, Van den Wildenberg, & Ridderinkhof, 2003; Yeung, Botvinick, & Cohen, 2003); the feedback ERN, which is elicited by error feedback (Miltner, Braun, & Coles, 1997); and the medial frontal negativity, which is associated with reward processing (Gehring & Willoughby, 2002). However, morphological and functional similarities between these components have led to debates about their ontological status, particularly whether various pairs of the components are different manifestations of the same underlying phenomenon. These debates include discussions about the relationship between the response ERN and the feedback ERN (Miltner et al., 1997; Holroyd & Coles, 2002), the response ERN and the N200 (Yeung, Botvinick, et al., 2003), the response ERN and the CRN (Coles, Scheffers, & Holroyd, 2001; Vidal, Burle, Bonnet, Grapperon, & Hasbroucq, in press), the feedback ERN and the medial frontal negativity (Holroyd, Coles, & Nieuwenhuis, 2002; Nieuwenhuis, Yeung, Holroyd, Schurger, & Cohen, 2003), and the oddball N200 and the no-go N200 (Nieuwenhuis, Yeung, Van den Wildenberg, et al., 2003). Fundamental theoretical and methodological issues hinge on the resolution of these questions.

In this paper I highlight the ambiguous relationship between another pair of ERP components, the feedback ERN and the oddball N200. First, I examine empirical evidence addressing whether or not the two components reflect the same phenomenon. I argue that the evidence is insufficient to conclude that the components are produced by different cognitive processes. Then, I explore the consequences of two possibilities: In case the two ERP components are distinct phenomena, I discuss methods for their empirical dissociation, and in case the two ERP components are the same phenomenon, I speculate about a possible unifying theory. Although the question about the relationship between the oddball N200 and the feedback ERN remains open, I hope that this paper will encourage careful examination of the assumptions that underpin studies of these components.

The oddball N200 and the feedback ERN: Same or different?

A fundamental assumption of ERP research is that the ERP can be separated into different components, each indexing the degree of activity of a particular cognitive function. The task of the experimenter is to identify the conditions that invoke the function, the type of data that the function processes, and the nature of the computation performed by the function (Donchin, Karis, Bashore, Coles, & Gratton, 1986). In this view, each ERP component is defined by its amplitude, polarity, latency, and scalp distribution which, by systematic experimental manipulation, can be shown to be functionally related to the underlying cognitive process (Coles & Rugg, 1995; Donchin, Ritter, & McCallum, 1978). Furthermore, two ERP components are said to be different from one another only in so far as the features associated with the components can be independently varied, providing evidence that the two components are generated by different cognitive processes. In practice, ERP components are typically distinguished by their different latencies, polarities, and/or scalp distributions, with variance in the amplitude of each component indicating the degree of activation of the associated cognitive process. For example, although they share the same polarity and similar latencies, the “P3b” and the “novelty P3” are distinguished by their different scalp distributions and by the way in which the amplitudes of these components respond to experimental variables (Spencer, Dien, & Donchin, 2001).

What, then, to make of the oddball N200 and the feedback ERN? Several varieties of N200 have been described in the literature (for review see Pritchard, Shappell, & Brandt, 1991); the oddball N200 refers to a frontal-central negativity elicited by infrequent events, particularly in the so-called

“oddball” paradigm in which subjects are presented with a series of stimuli and are required to count the occurrences of a target stimulus (e.g., Towey, Rist, Hakerem, Ruchkin, & Sutton, 1980).

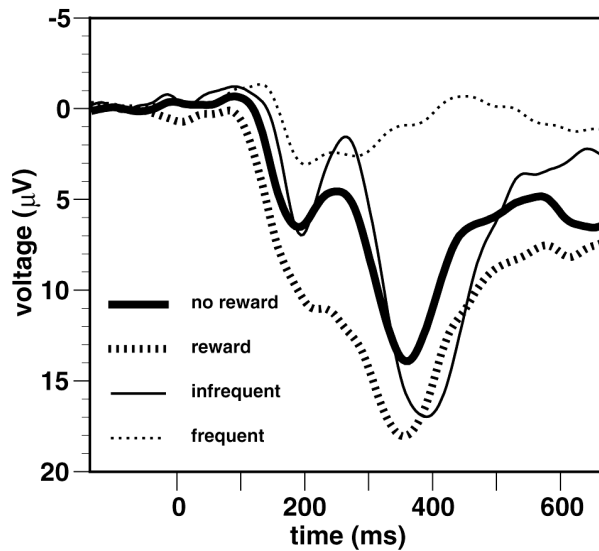


Figure 1.

ERPs elicited by imperative stimuli in an oddball task and by feedback stimuli in a reinforcement learning task. “Infrequent, frequent”: ERPs elicited by the target (10% of trials) and non-target (90% of trials) stimuli, respectively, in the oddball task. “reward, no reward”: ERPs elicited by feedback stimuli indicating rewarded trials and non-rewarded trials, respectively, in the reinforcement learning task. Stimulus onset occurs at 0 ms. The oddball N200 on infrequent trials and the feedback ERN on no reward trials can be seen peaking at about 250 ms. The data from both tasks were recorded in the same group of subjects at channel FCz (Holroyd, Larsen, & Cohen, in press; the “reward” and “no reward” outcomes correspond to the maximum and minimum rewards in the “win” condition of that study).

The hallmark of this negative component is that its amplitude increases as the eliciting stimulus occurs less frequently (e.g., Squires, Wickens, Squires, & Donchin, 1976; Duncan-Johnson & Donchin, 1977). Figure 1 illustrates ERPs elicited by target (“infrequent”) and non-target (“frequent”) stimuli when subjects were instructed to count the occurrence of a stimulus that occurred at random on 10% of the trials. The oddball N200 peaks about 260 ms following the onset of the infrequent stimulus; Figure 2 illustrates that this component, measured base-to-peak, exhibits a frontal-central scalp distribution. In contrast to the oddball N200, the feedback ERN is elicited by feedback stimuli that indicate that an unfavorable outcome has occurred, but not by stimuli that indicate that a favorable outcome has occurred (Miltner, Braun, & Coles, 1997; Holroyd & Coles, 2002; for review see Holroyd, Nieuwenhuis, Mars, & Coles, in press; Nieuwenhuis, Holroyd, Mol, & Coles, 2003). Figure 1 illustrates ERPs elicited by feedback stimuli indicating favorable (“reward”) and unfavorable (“no reward”) outcomes in a trial-and-error learning task, in the same group of subjects that participated in the oddball task. The feedback ERN can be seen as the negativity peaking about 250 ms following stimuli indicating the absence of a reward; Figure 2 shows the scalp distribution of this component.

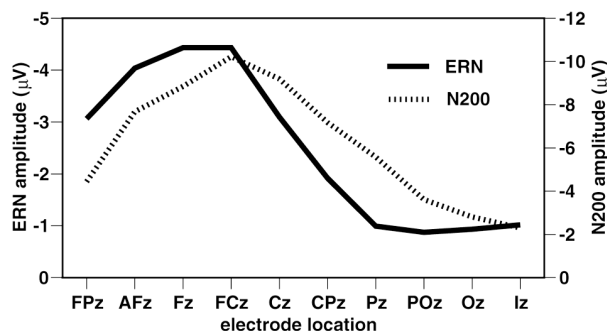


Figure 2.

Scalp distributions of the oddball N200 and feedback ERN data associated with Figure 1. Electrode locations are labeled according to the 10-20 system for electrode placement. The distributions of the oddball N200 and the feedback ERN peak at frontal-central scalp locations. Note the different scales for the two components. Amplitudes were measured base-to-peak as described in Holroyd, Nieuwenhuis, Yeung, et al. (in press).

Clearly, the oddball N200 and the feedback ERN share similar morphologies: They are identical in polarity, they reach maximum amplitude at about the same time following stimulus presentation, and they peak at frontal or frontal-central scalp areas. These similarities raise the question of whether the two components are in fact produced by distinct cognitive processes. On the other hand, the feedback ERN appears to be distributed across slightly more anterior areas of the scalp relative to the oddball N200. However, given the difference in scale between the two components (the oddball N200 is about twice the size of the feedback ERN here), it is difficult to evaluate whether the difference in the distributions is real or whether it stems from a measurement artifact. Perhaps more convincingly, the amplitudes of the two components have been functionally dissociated, suggesting that they indeed reflect different phenomena. Specifically, the amplitude of the feedback ERN is larger for unfavorable events than for favorable events, even when the frequencies of both events are the same (Miltner et al., 1997; Holroyd & Coles, 2002; Holroyd, Nieuwenhuis, Yeung, Cohen, in press), but the oddball N200 is larger for infrequent events than for frequent events, in conditions (such as the oddball paradigm) in which rewards and punishments play no obvious role (e.g., Towey et al., 1980). Thus, the amplitudes of these negativities can be exercised along two independent dimensions: one dimension in which outcomes are favorable or unfavorable, and a second dimension in which outcomes are frequent or infrequent. These findings suggest the existence of two systems, one involved in reward or performance processing and a second sensitive to stimulus frequency. By contrast, the latency and scalp distribution of the medial frontal negativity are comparable to those of the feedback ERN, and a failure to dissociate the two components functionally suggests that the two waveforms are the same phenomenon (Nieuwenhuis, Yeung, Holroyd, et al., 2003; see also Holroyd et al., 2002).

This issue is of concern because feedback stimuli provide both frequency and valence information, and thus can be expected to produce both an N200 and an ERN, complicating the interpretation of the waveforms. Despite their functional dissociation, the remarkable similarity between the morphologies of the oddball N200 and the feedback ERN, together with their frequent co-occurrence, raises the question of whether or not they are actually the same thing. To illustrate by analogy, the amplitude of the P300 is sensitive to both stimulus probability and “stimulus meaning” (Johnson, 1988), yet apparently no one has proposed that these two factors elicit different ERP components with identical polarities and with highly similar latencies and scalp distributions. Instead, it is often suggested that P300 amplitude reflects an underlying cognitive process that is sensitive to both factors (e.g., Johnson, 1988). Likewise, it is important to consider the possibility that the feedback ERN and oddball N200 reflect the operation of a common underlying mechanism that is sensitive to both stimulus probability and valence. In what follows, I explore the consequences of both of these possibilities. First, if these two negativities are indeed different, and thus produced by separate cognitive processes, then how can either be used to measure the cognitive process of interest without contamination of the measurement by the other process? Second, if these negativities reflect the same phenomenon, and are not in fact produced by separate cognitive processes, then what is the cognitive process that gives rise to them? The first possibility entails carrying out carefully designed experiments that tease apart the relative contributions of each of these components to the ERP, whereas the second possibility entails the development of a general theory that predicts the amplitude of the negativity in both feedback tasks and oddball tasks.

If the oddball N200 and feedback ERN are different things

How could the oddball N200 and feedback ERN have similar scalp distributions and latencies, yet be generated by different processes? Of course, both components could be elicited by separate functions (one that is sensitive to stimulus frequency, the other that is sensitive to stimulus valence) implemented in nearby areas of cortex (accounting for the similar scalp distributions) that are simultaneously invoked by the activation of a common neural input (accounting for the similar

latencies). The ERPs generated by these two events would summate at the scalp according to the principle of superposition.

It follows that one cannot measure the amplitude of the negativity elicited by error feedback and assume that the measure is sensitive only to the activation of the reward processing system, rather than also to a system that is sensitive to stimulus frequency (and not reward). This problem cannot be ameliorated with the application of sophisticated data analysis techniques for ERP decomposition, such as principal components analysis, because these techniques fail when the ERP components share highly similar latencies and scalp distributions (for review see Donchin & Heffley, 1978). In general, the absolute activation of a cognitive process cannot be inferred from the amplitude of an ERP component associated with a single experimental condition; rather, the relative activation of that process should be inferred by comparing the data associated with different experimental conditions (as is the practice in hemodynamic neuroimaging studies). The straightforward way to do so, of course, is to compare the amplitude of the ERP component across two experimental conditions, where the difference between the conditions is assumed to affect only the cognitive process of interest. In the case of the feedback ERN, the component was identified by comparing the ERP elicited by error feedback with the ERP elicited by correct feedback, where both error and correct feedback occurred on 50% of the trials (Miltner et al., 1997). This comparison ensured that the impact of stimulus frequency on the ERP was equivalent across conditions.

However, some experimental manipulations necessarily affect two (or more) cognitive processes, in which case the relative activation of one process cannot be inferred by comparing the ERPs associated with two experimental conditions. Instead, if the manipulation can be assumed to affect only two cognitive processes, then the activity associated with the cognitive process of interest can be identified with a 2-factor design. To explain by example, in a recent study participants engaged in a guessing task with two conditions: In one condition rewarded trials were frequent and non-rewarded trials were infrequent, whereas in a second condition rewarded trials were infrequent and non-rewarded trials were frequent (Holroyd, Nieuwenhuis, Yeung, et al., in press; see also Butterfield & Mangels, 2003). We wanted to dissociate reward-related activity associated with the feedback ERN from frequency-related activity associated with the oddball N200. To do so, we measured base-to-peak the amplitude of the negativity elicited by all four feedback types: frequent rewards, frequent non-rewards, infrequent rewards and infrequent non-rewards. We then compared the difference between the measures associated with infrequent rewards and infrequent non-rewards with the difference between the measures associated with frequent rewards and frequent non-rewards. This comparison showed that infrequent outcomes tended to elicit greater activation of the reward processing system than frequent outcomes, while controlling for the baseline effects of stimulus frequency on the ERP.

In some tasks the frequency of occurrence of the feedback stimuli cannot be easily counterbalanced across conditions, however. In such cases, the investigator may consider running an oddball task as a separate condition, in which the probability of the infrequent target stimulus is matched to the probability of the negative feedback stimulus in the feedback task. In this way, the amplitudes of the negative ERP components elicited by the negative feedback stimuli and by the infrequent target stimuli can be compared. This procedure was followed in a recent study; the amplitude of the feedback ERN was found to be larger than that of the oddball N200, which provided a measure of stimulus valence that was independent of stimulus frequency (Yeung, Holroyd, & Cohen, 2003).

It is worth noting that measurement of the feedback ERN is complicated by component overlap with the P300, which occurs immediately following the N200 and which is distributed over posterior areas of the scalp (for review see Donchin & Coles, 1988). However, contrary to what one might assume, the absence of the feedback ERN on correct trials does not appear to result from overlap with this positive-going component. In fact, the amplitude of the P300 tends to co-vary with the amplitude of the oddball N200: Both increase as the eliciting stimulus occurs less frequently. Historically, the amplitudes of the two components were seen to be so highly correlated

that they were said to form an “N200-P300 complex” (e.g., Squires et al., 1976; Duncan-Johnson & Donchin, 1977). Thus, it is unclear how the absence of the feedback ERN on correct trials could result from component overlap with the P300, since large P300s are normally associated with a negativity in the time range of the feedback ERN. Consider the ERP elicited by infrequent rewards. Although infrequent events in general elicit both a P300 and an oddball N200 (cf. Figure 1), infrequent rewards elicit the P300 but do not elicit the N200; indeed, they seem to elicit a positivity during that time period instead (Holroyd, Nieuwenhuis, Yeung, et al., in press). This result suggests that the absence of the feedback ERN on the rewarded trials is not simply due to component overlap with the P300. Rather, it is due to the absence of the negativity itself.

If the oddball N200 and feedback ERN are the same thing

Of course, these worries assume that the oddball N200 and the feedback ERN are indeed produced by different cognitive processes. However, in principle the feedback ERN and the oddball N200 could be produced by a single process. In this case, the apparent functional dissociation between the oddball N200 and the feedback ERN would belie a deeper unifying principle. More generally, as noted above, the recent ERP literature on cognitive control has described a plethora of negative ERP components perceived to be functionally and/or morphologically related: the feedback ERN, the response ERN, the CRN, the N200, and the medial frontal negativity. A fruitful approach might entail bringing some of these seemingly disparate phenomena under the umbrella of a single theory. This approach is a guiding principle of other scientific disciplines, most famously in physics, so it would seem to be a wise example to follow.

In keeping with this approach, the reinforcement learning theory of the ERN attempted to unify both the response ERN and the feedback ERN in a single conceptual framework by proposing that both components were produced by a common dopamine-related process (Holroyd & Coles, 2002). With regard to the N200, furthermore, Yeung and colleagues have attempted to unify the N200 with the response ERN in a single theory (Yeung, Botvinick, et al., 2003). The N200 and the response ERN share similar scalp distributions and equivalent dipole sources, and Yeung and colleagues have proposed that both of these negativities are produced by the simultaneous activation of incompatible response channels (called “response conflict”). Similarly, Nieuwenhuis and colleagues have argued that the oddball N200, which is associated with infrequent stimuli in oddball tasks, is actually the same as the “no-go N200”, which is associated with infrequent no-go responses in go/no-go tasks (Nieuwenhuis, Yeung, Van den Wildenberg, et al., 2003). Although the conflict theory in present form depends explicitly on response conflict, in principle it can also be made to account for the oddball N200, in which no overt response is produced (Yeung, Botvinick, et al., 2003).

We are currently investigating the extent to which the conflict and reinforcement learning theories make identical predictions, and the extent to which the two theories are fundamentally different (Holroyd, Yeung, Coles & Cohen, 2003; see also Holroyd & Yeung, 2003). This effort affords the hope that the N200, the response ERN, and the feedback ERN could be unified in a single theory. Although the form that such a theory might take is still difficult to imagine, the following possibility suggests itself. According to the reinforcement learning theory of the ERN, error signals conveyed by the mesencephalic dopamine system modulate the activity of a region of anterior cingulate cortex associated with cognitive control of motor behavior. The theory is predicated on the observation that phasic increases and decreases in the activity of mesencephalic dopaminergic neurons appear to indicate that ongoing events are, respectively, “better than expected” and “worse than expected” (for a review of the phasic activity of the midbrain dopamine system, see Schultz, 2002). Furthermore, the theory holds that variation in ERN amplitude is produced by the impact of these phasic dopamine error signals on this motor-related region of anterior cingulate cortex (where the ERN appears to be generated; e.g., Miltner et al., 1997), with decreases in phasic dopamine associated with larger ERN amplitudes and increases in phasic dopamine associated with smaller ERN amplitudes.

For the purposes of this discussion, the critical point is that dopamine modulates the activity of anterior cingulate cortex. Specifically, via dopamine D1 receptors, dopamine appears to “focus” or “sharpen” the effects of synaptic inputs on the apical dendrites of anterior cingulate motor neurons (Yang & Seamans, 1996), a process that could also modulate the amplitude of ERP components (Holroyd & Coles, 2002). Thus, if anterior cingulate cortex produced the oddball N200 (as it appears to; Nieuwenhuis, Yeung, Van den Wildenberg, et al., 2003), then the variation in ERN amplitude could reflect dopamine-induced modulation of the amplitude of that negativity. Put another way, the activity of anterior cingulate cortex could establish a “baseline” negativity (the oddball N200) that is modulated by the reward-related information conveyed by the dopamine system. The difference in the ERP associated with the feedback ERN between rewarded trials and non-rewarded trials could then reflect dopamine-related modulation of the amplitude of this baseline negativity. In fact, although the dopamine theory of the ERN has emphasized the possibility that the ERN is produced by disinhibition of anterior cingulate cortex on error trials, it is equally compatible with the possibility that the oddball N200 is suppressed by inhibition of anterior cingulate cortex on correct trials. In this view, the baseline negativity would be extinguished by reward-related activity on trials with unpredicted positive outcomes.

Note that this idea follows directly from the reinforcement learning theory of the ERN, but it is not a unified theory of the feedback ERN and the oddball N200. This is because the theory is independent of the actual role played by anterior cingulate cortex and of the functional significance of the baseline negativity. As such, the theory predicts the size and direction of the difference in the amplitude of the ERP between correct trials and error trials, but the theory makes no prediction about the absolute amplitude of the negativity on these trials. In contrast, a unified theory of the oddball N200 and the feedback ERN would predict the amplitude of the negativity even in conditions in which rewards and punishments played no obvious role. This requirement would entail the integration of the reinforcement learning theory of the ERN with a theory of the oddball N200 that predicts N200 amplitude. Of course, such a theory of the N200 already exists: the conflict monitoring theory (Yeung, Botvinick, et al., 2003; see also Nieuwenhuis, Yeung, Van den Wildenberg, et al., 2003). If anterior cingulate cortex is activated by conflict, as proposed by the conflict theory, and if dopamine modulates the activity of anterior cingulate cortex, as proposed by the reinforcement learning theory, then a theory that proposed dopaminergic modulation of conflict activity in anterior cingulate cortex might account for both the oddball N200 and the feedback ERN.

Conclusion

The oddball N200 and the feedback ERN are often implicitly assumed to be produced by different cognitive processes, but the truth of this assumption remains to be determined. It is important that studies that assume that the components are different make this assumption explicit, and that they carefully disassociate the contribution of the two components to the ERP. At the same time, it seems prudent to explore the possibility that the two components reflect different aspects of a common underlying cognitive process. This possibility would entail the development of a theory that accounted for both of the waveforms. Although the nature of such a theory is a matter of speculation, similarities between the oddball N200 and the feedback ERN are suggestive in this regard.

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