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Relevance and uncertainty jointly influence reward anticipation at the level of the SPN ERP component

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ABSTRACT

The stimulus-preceding negativity (SPN) component reflects the anticipatory phase of reward processing. Its amplitude is usually larger for informative compared to uninformative upcoming stimuli, as well as for uncertain relative to predictable ones. In this study, we sought to assess whether these two effects, when combined together, produced a synergistic effect or rather independent ones on the SPN during performance monitoring. Participants performed a speeded Go/NoGo task while 64-channel EEG was recorded concurrently. We focused on the SPN activity generated in anticipation of feedback, which was either positive (for correct and fast reactions) or negative (for correct but slow responses). Further, the feedback's informativeness about the satisfaction status of goals was alternated across blocks. When uncertainty about the action outcome was low (in conditions where positive feedback was either less or more frequent than negative feedback), the SPN amplitude (measured at fronto-central electrodes) did not vary as a function of feedback's relevance or valence. By comparison, when positive and negative feedback were equiprobable (uncertainty was high), the SPN was more pronounced for relevant compared to irrelevant feedback. Interestingly, in this condition, it was also larger at right fronto-central sites for positive than negative feedback. These ERP results suggest that both factors–relevance and uncertainty– combine and influence reward anticipation at the SPN level.

1. Introduction

During performance monitoring, both internal (motor) and external (feedback) cues are usually processed and used to adjust behavior when mismatches between goals and actions are detected. Several studies using the event-related potentials (ERP) technique have previously shown that the feedback-related negativity (FRN) component reflects external feedback information processing during performance monitoring. According to the dominant account, the FRN reflects a phasic reward prediction error signal generated by specific fronto-striatal loops (Holroyd and Coles, 2002; Holroyd et al., 2008; Sambrook and Goslin, 2015; Walsh and Anderson, 2012). When the performance or evaluative feedback conveys information about an unexpected mismatch between the hoped-for and the actual outcome, a negative-going wave is elicited over fronto-central locations, peaking at around 250 ms post-feedback onset at Fz or FCz sensors. In line with the reward prediction error account, FRN amplitude is larger for unexpected relative to expected events (Hajcak et al., 2007; Pfabigan et al., 2011; von Borries et al., 2013), and for worse-than-expected events, that is, for negative compared to positive performance feedback (Miltner et al., 1997; Nieuwenhuis et al., 2004).

Performance monitoring is a process which is highly dynamic and flexible, seeking to exploit the most informative cue available at a given time and avoiding redundancy (Holroyd and Coles, 2002; Ullsperger et al., 2014). In a situation where the processing of external feedback information is impossible (i.e., feedback information is not available or is perceived as unreliable), the processing of internal (i.e., motor response-based) events prevails and is used to guide the course of performance monitoring. In this situation, the error-related negativity (ERN) component indexing the early, perhaps automatic, detection of response errors based on a swift comparison between the intended and actual motor response is usually elicited at the same fronto-central electrode positions (Falkenstein et al., 1991; Gehring et al., 1993; Ullsperger et al., 2014).

Performance monitoring is not only based on phasic (and reactive) reward prediction error effects upon response execution (ERN) or feedback processing (FRN), but it also usually operates based on additional cues that occur after the response but before the outcome, and that are mostly proactive and anticipatory in nature (hence are less phasic and more sustained than the ERN or FRN). Indeed, several

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earlier ERP studies have identified an ERP component occurring after response execution and during feedback anticipation,[1] called the stimulus-preceding negativity (SPN; Brunia, 1988; Brunia and van Boxtel, 2001; Brunia et al., 2011; Chwilla and Brunia, 1991). The SPN amplitude typically increases from parietal or central to frontal locations, with a right hemispheric dominance usually observed over (pre)frontal areas (F4 vs. F3), consistent with a putative main intracranial generator in the right anterior insular cortex (Brunia, 1988; Brunia et al., 2000, 2011). Even though the SPN has been much less explored in the existing literature than the ERN or FRN components (especially in relation to performance monitoring processes), some studies have already shed light on its putative function. According to the most dominant (motivation-based) model, the SPN is a neurophysiological marker of the anticipation of meaningful information (Brunia and van Boxtel, 2001; Brunia et al., 2011; Kotani et al., 2001, 2003; Masaki et al., 2006, 2010; Ohgami et al., 2004, 2006; van Boxtel and Böcker, 2004). This model predicts a larger and more negative SPN for the anticipation of stimuli that are deemed highly informative compared to ones that carry less information. In line with this, several ERP studies confirmed that the anticipation of stimuli that are informative about rewards and punishments (including monetary gain, evocative photos, or electric shocks) led to a more pronounced SPN component, compared to the anticipation of stimuli considered uninformative or less informative (Kotani et al., 2009; Masaki et al., 2006; van Boxtel and Böcker, 2004).

In performance monitoring research, performance feedback is a good example of a highly informative stimulus. In accordance with this notion, Masaki et al. (2010) reported a larger SPN in response to the anticipation of an action-contingent positive feedback (i.e., monetary gain) compared with a reward feedback that was non-contingent on the preceding action. This and other findings have led to the consensus in the psychophysiology literature that the SPN component reflects the anticipation of informative events (Brunia, 1988; Chwilla and Brunia, 1991). It remains currently unclear, however, what "informative" means in this specific framework, especially when it comes to dissecting possible performance monitoring processes at stake during feedback/outcome anticipation.

In previous work (Walentowska et al., 2016), we conceptualized informativeness within the notion of goal relevance (see also Moors, 2007). We distinguished between three separate, but related, meanings of goal relevance: (i) task relevance, which means that a stimulus signals an opportunity to implement goal-directed behavior, which may or may not lead to goal satisfaction; (ii) informativeness, or the degree to which a stimulus is informative about the satisfaction status of pursued goals; and (iii) the impact that a stimulus has on these pursued goals. Feedback stimuli are especially deemed goal relevant in the second and/or third sense. They usually come with a degree of informativeness or trustworthiness (Walentowska et al., 2016), and they can impact on goals to a variable extent (from little to a lot; see also Severo et al., 2017). Note that the type of informativeness at stake here is not simply of any type, but one that conveys information on the satisfaction status of goals. Taking a closer look at previous performance monitoring research studying the role of the SPN component, it seems that informativeness was used there in exactly this second sense. Indeed, in the study of Masaki et al. (2010), performance feedback either did or did not inform the actor about the degree to which his/her action corresponded to an intended action; hence this feedback varied with respect to whether it was informative about the satisfaction status of the goal to engage in the action. Moreover, if the intended action was at the service of higher-order goals, such as the goal to earn money or social status, the performance feedback not only informed the actor about the satisfaction status of the goal to perform well on a particular trial or the task as a whole, but also about the satisfaction status of these higher-order goals (Severo et al., 2017). In this paper, we focus on informativeness as it relates to goal relevance in the second sense. From now on, we refer to this type of informativeness as goal relevance or relevance.

Previous work (Walentowska et al., 2016) already showed that the FRN component (differentiating positive from negative feedback) was elicited when the performance feedback was perceived as goal relevant by the participants but not when it was perceived as irrelevant. Based on these findings, we formulated the prediction that goal-relevant feedback could also elicit a larger SPN component than goal-irrelevant feedback. This was the first prediction that we aimed to test in the current study.

Informativeness as it relates to goal relevance is not the only factor used by performance monitoring brain systems during feedback anticipation. Another factor that is very likely to influence this processing stage, but that is rather poorly explored in the existing ERP literature on performance monitoring, is the perceived probability and hence (un)certainty about the upcoming performance feedback. In classical information theory, the notion of uncertainty is linked to the notion of informativeness. As postulated by Shannon (1948), information can be thought of as the resolution of uncertainty. "Information" is a set of possible messages, which should be sent over a noisy channel, and reconstructed by the receiver with low probability of errors, despite the channel noise. The key measure in information theory is "entropy", which quantifies the amount of uncertainty or randomness before an outcome is revealed and hence the degree of information that is carried by the outcome once it is revealed. For example, the coin flip with two equally likely outcomes and hence less uncertainty leads to an outcome with less information (lower entropy) than the roll of a die with six equally likely outcomes and hence more uncertainty. Classical information theory thus entails that the higher the entropy is, the more uncertain the outcome is before it is revealed, and the more information the outcome therefore provides once it is revealed (see also Luce, 2003).

The link between uncertainty and informativeness is also exemplified in animal and human brain studies, in which it has been demonstrated that uncertainty (e.g., the volatility of stimulus-outcome associations) and curiosity play a central role in estimating and learning actions (Bennett et al., 2016; Kidd and Hayden, 2015), with a dominant role of the anterior cingulate cortex in decision making and reward processing (Behrens et al., 2007). Interestingly, Bach and Dolan (2012) identified the (anterior) insula as an important limbic structure within a distributed brain network directly involved in computing uncertainty. Given that the (right) anterior insular cortex is thought to be one of the main intracranial generators of the SPN component (Brunia, 1988; Brunia et al., 2011), it is conceivable that uncertainty processing influences the SPN during feedback anticipation.

Some recent ERP studies have already provided support for the notion that the amplitude of the SPN component is related to uncertainty or unpredictability. Their results showed that the amplitude of the SPN was systematically larger in situations where participants anticipated unpredictable (Catena et al., 2012; Morís et al., 2013) or unexpected reward (Fuentemilla et al., 2013) compared to feedback that was highly predictable or expected. Accordingly, we can derive the prediction that uncertainty should augment the size of the SPN during feedback anticipation. This prediction constituted the second hypothesis tested in the present study.

When positive and negative feedback following action execution are equiprobable, uncertainty about the action outcome is the highest. However, when uncertainty about the action outcome is reduced, the predicted increase in SPN may result not only from low uncertainty but also from changes in motivation in the low reward probability condition, in which negative feedback dominates over positive feedback. In this condition, not only the uncertainty is lower compared to the equiprobable condition, but defensive motivation is also likely to prevail. Because defensive motivation can influence performance

[1] This is especially true when the feedback is contingent on behavioral performance and/or motor responses.