

## Invited review

## Waiting to perceive: Reward or punishment?

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## ABSTRACT

Neurobiological accounts of the dopaminergic reward system and psychophysiological explanations of the error-related negativity (ERN) both emphasize the comparison of expected versus actual outcome for voluntary actions. The stimulus-preceding negativity (SPN) constitutes a valuable index of that expectation, in that it has high temporal resolution and its anatomical, cognitive and affective correlates have been reasonably well characterized. This review links established findings regarding the SPN to current research on the dorsal and ventral attention systems, somatic marker hypothesis, ERN, the reward system and relevant neurological and psychiatric findings. Special emphasis is given to the pre-feedback SPN and its origin within anterior insular cortex.

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## 1. Introduction

Emergence of the error-related negativity (ERN, Gehring et al., 1993; formerly  $N_E$ , Falkenstein et al., 1991) as one of the most widely studied event-related potentials (ERP) portends an end to dominance of the “cold cognition” approach to electrophysiology. By integrating the concepts of hedonic value and reward into the information processing tradition, this line of research has helped link the disparate fields of affective and cognitive neuroscience.

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Based on neurobiological research on the reward system, Holroyd and Coles (2002) proposed that the ERN reflects a comparison between anticipated and actual outcome. To complement the ERN and better understand the neural basis of reinforcement, it would be useful to have an electrophysiological measure of this anticipation (Masaki et al., 2006). The main purpose of the present review is to argue that the stimulus-preceding negativity (SPN, Damen and Brunia, 1987) constitutes such a measure.

The pre-feedback SPN is a slow, right-hemisphere dominant, negativity that builds in size as the arrival of a feedback display grows imminent. As with most slow waves, it is generated by multiple neocortical sources. The second purpose of this review is to describe attempts to fractionate the SPN into subcomponents that

reflect cognitive and affective processes arising from distinct sources within the brain. We begin with a description of how the SPN was itself discovered during attempts to fractionate the CNV (contingent negative variation; Walter et al., 1964).

## 2. Isolating the SPN from the CNV

In many sports the competition starts with a *get-set* and a *go* signal. Having reached the finish line, sports men and women wait for the announcement of the score. Translated into the electrophysiological laboratory situation, the first condition goes along with the CNV, while the second condition goes along with another slow potential, the stimulus-preceding negativity. Both are anticipatory slow waves, as is the *Bereitschaftspotential* (BP, Jahanshahi and Hallett, 2003; Kornhuber and Deecke, 1965; Shibasaki and Hallett, 2006).

Negative slow potentials are thought to arise typically from the summation of excitatory post-synaptic potentials within the apical dendrites of pyramidal cells that are arranged in columns within the cerebral cortex (Rockstroh et al., 1989). Preceding a simple unilateral movement the BP is present bilaterally over the cortical motor areas, with larger amplitudes over the hemisphere contralateral to the movement side prior to finger movements but ipsilateral to the movement side prior to foot movements. This paradoxical distribution indicates that the BP is not a general index of movement preparation, but a reflection of activity in small areas in the motor cortex, in conformity with the representation of the homunculus (Penfield and Boldrey, 1937).

From the beginning it was clear that BP and CNV must represent different processes, since their topographical distributions differed. The CNV is manifest during the foreperiod, the interval between a warning signal and imperative stimulus. This large negative wave was originally considered an expectancy component, but it seemed also to be related to response preparation, and thus, to have something in common with the BP. That problem was partly clarified by the use of longer foreperiods. Connor and Lang (1969) discovered the existence of two phases of the CNV, an early wave, related to the alerting properties of the warning signal and a late wave related to response preparation. The potential distribution of the early and late wave differed again, the early wave being larger over the frontal areas and the late wave being larger over the central (motor) areas. The paradoxical topography found with the BP was also present with the late wave (Brunia and Vingerhoets, 1980), suggesting that the terminal portion of the CNV reflected motor preparation. Moreover, preceding fast responses the late wave showed larger amplitudes than preceding slow responses (Brunia and Vingerhoets, 1981).

Although such evidence suggests that the late CNV is motor-related, there is nonetheless an important difference with respect to the BP. Brunia and Vingerhoets (1981) asked their subjects to make a voluntary movement, which triggered the presentation of a visual stimulus 4 s later, upon which the same movement had to be made again. The first movement was preceded by a BP, the second by a CNV late wave. The two waves showed similar scalp distributions, but the CNV late wave was always larger in amplitude than the BP, suggesting that it reflects more than just motor preparation. The question was what this extra negativity might reflect.

The CNV late wave was hypothesized to represent at least two processes, anticipatory attention for the imperative stimulus and preparation of the movement. The two processes are intermingled and cannot be separated in time, so it may never be possible to unequivocally interpret experiments that use the classical CNV paradigm. In an attempt to get rid of the movement preparation, investigators tried asking subjects to postpone their response. However, since movement preparation can start more than 1.5 s prior to execution, this approach was unconvincing.

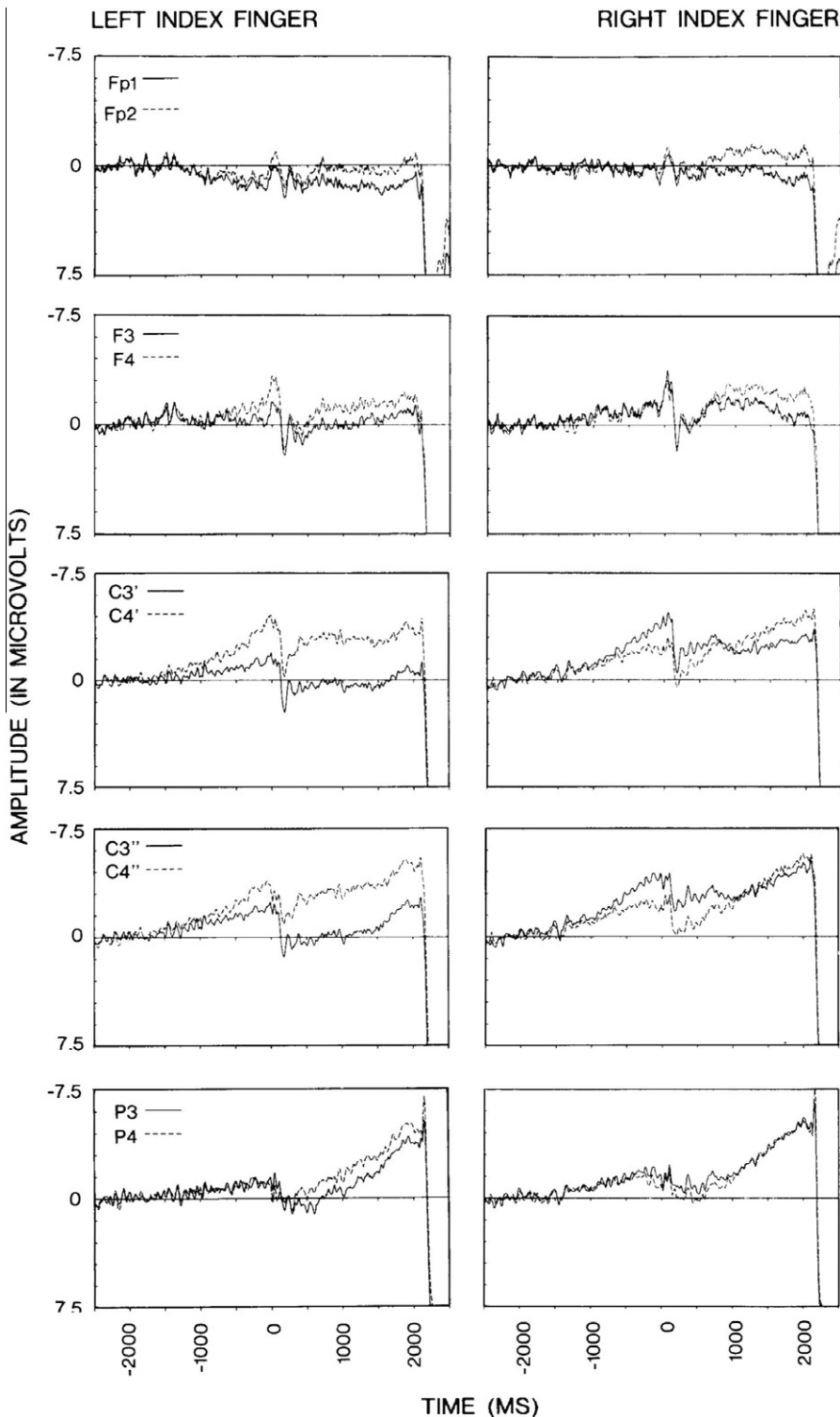
Another approach toward distinguishing motor and attention subcomponents of the CNV has involved direct recordings from the cortical surface. The group of Shibasaki and Ikeda has published a number of subdural experiments relevant to fractionating the CNV. They contrasted two different warned reaction time (RT) tasks with relatively short intervals (2 s) between S1 and S2. In the *S1 choice task*, the first stimulus serves as a cue indicating whether S2 will be a Go or No-Go stimulus. If S1 announces a No-Go trial there should be minimal response preparation or attention prior to S2 and, consequently, little or no slow wave activity. If S1 announces a Go stimulus then the trial is transformed into a warned, simple-RT task which should be accompanied by a CNV. In their *S2 choice task*, the first stimulus is a neutral warning signal that merely predicts the time of onset for the second stimulus. Hence, subjects remain uncertain about which particular S2 will occur and which action, Go or No-Go, will be required. This should also elicit a CNV, but one that reflects a more diverse profile of anticipatory processes.

In a study by Ikeda and colleagues (1996), subdural electrodes were placed in the bilateral mesial prefrontal and orbitofrontal area, the SMA, and MI. The authors concluded, congruent with Brunia (1988), that the scalp-recorded CNV is 'actually a sum of two potentials, namely the slow preceding potential before S2 generated in the prefrontal region and the BP generated in the SMA and MI'. In a further study from the same laboratory, Hamano and coworkers (1997) used a larger set of subdural electrodes and concluded that the CNV late wave is a multi-source phenomenon, in which prefrontal, mesial temporal and occipital areas were involved. With respect to trials in which S1 signaled a No-Go response, Ikeda and colleagues (1999) observed slow waves at pre-SMA and prefrontal areas. The authors suggested that these might well be related to 'general anticipation or attention for the forthcoming stimuli'.

Using conventional EEG recordings, Brunia and Damen (1988; Damen and Brunia, 1987) developed an alternative method to separate the attention and motor components, the time estimation task. Initially, they asked participants to press a button at 20-s intervals. Performance feedback was delivered 2 s after each button press. Thus anticipatory attention and motor preparation were separated in time. As expected, the button press was preceded by a BP and the feedback signal by an SPN. The feedback signal provided subjects with information about the accuracy of their performance. (In experimental psychology this has historically been referred to as *Knowledge of Results*, KR, an expression that is often used interchangeably with *feedback*.) The topographical distribution of the two slow waves was again different. The BP was larger over the hemisphere contralateral to the side of finger movement, whereas the SPN was larger over the right hemisphere. The SPN showed sustained negativity over prefrontal cortex and a sharply increasing negativity over parietal cortex (see Fig. 1).

In subsequent studies, the paradigm was changed slightly. Instead of emitting the response at regular 20-s intervals further, participants received a start signal that indicated the beginning of the interval (e.g., 3 s) that they were to terminate with a key press. Two seconds after the key press, a feedback display indicated whether the response was too early, too late, or just in time. The definition of "just in time" could be adjusted to manipulate task difficulty.

Although features such as these helped establish the time estimation paradigm as standard for research on the SPN, there was good reason for confidence in the component's generality. Stimulus-preceding negativities had by this time also been documented prior to feedback in motor aiming tasks (Grünewald and Grünewald-Zuberbier, 1983) and prior to emotion-inducing slides in a non-task situation (Klorman and Ryan, 1980; Simons et al., 1979).



**Fig. 1.** Example of a typical stimulus-preceding negativity (SPN) recorded prior to feedback in a time estimation task. The participant's key press that terminated the estimated time interval was at Time 0 and feedback was displayed at 2000 ms. Note the larger amplitudes observed over right- as compared to left-hemisphere electrode sites (e.g., C4 and F4 vs. C3 and F3), as well as the steeper pre-feedback ascent at parietal as compared to prefrontal sites. (Adapted from Brunia and Damen (1988).)

### 3. The SPN depends on the type of anticipated information

Most studies published within the first few years after the identification of the SPN did not distinguish between different types of information that was anticipated. There seemed to be a unitary view of motor preparation and of stimulus anticipation. Preparation for a movement was accompanied by movement-preceding negativity (MPN, essentially the BP), anticipation of a stimulus

was reflected in the SPN, and the CNV was thought to be the sum of MPN and SPN (e.g., Brunia, 1988). Of course, this situation did not last long and researchers soon began to vary the type and amount of information of the stimulus that the SPN preceded.

Chwilla and Brunia (1991a) were the first to vary both the informational and motivational content of the stimulus in the time estimation task. Informational content was varied by presenting either no feedback, false feedback or true feedback to their

subjects. Motivational content was varied by either including or not including a monetary bonus. Chwilla and Brunia found an SPN only prior the real feedback. The authors concluded that the SPN was mainly influenced by the informational content of the stimulus, because presenting true or false feedback had a large effect on the SPN, whereas supplementing the feedback with monetary rewards only altered the component's scalp distribution.

Damen and Brunia (1994), on the other hand, doubted these earlier conclusions because presenting true, false, or no feedback does not just vary the informational content of the stimulus. Rather, it is such a fundamental manipulation for the execution of the time estimation task that many other variables are likely to be affected. Since conditions in Chwilla and Brunia's experiment were presented in blocks, subjects knew that in one condition the feedback was false. This could easily have reduced their interest in the feedback displays during those blocks.

Damen and Brunia (1994), therefore, devised a paradigm in which a time estimation task with feedback was contrasted with a situation in which an instructional stimulus contained information about the particular time interval to be produced. The subjects pressed a button to begin the trial. This was followed 2 s later by an instruction about the interval, after which another button had to be pressed. This was followed by a feedback display that indicated correctness of the key press. The investigators carefully corrected for any motor-related processes and found no appreciable SPN prior to the instruction stimulus. By contrast, a pronounced SPN with the typical scalp distribution was observed prior to feedback.

This was replicated by Kotani and Aihara (1999), who additionally noted that the pre-feedback but not the pre-instruction SPN was reduced when perceptual difficulty was augmented (see also Hillman et al., 2000). On the assumption that the SPN reflects anticipatory attention, one might expect that the SPN would be larger when the stimulus is difficult to perceive. Such findings motivate a more detailed examination of this aspect of the SPN.

The most obvious prediction one can make about a component hypothesized to reflect anticipatory attention is that its scalp distribution should vary according to the modality of the expected stimulus. With this in mind, Brunia and van Boxtel (2004) compared anticipation of auditory and visual feedback stimuli in the time estimation task. They found larger SPN amplitudes over the frontal cortex with auditory stimuli than with visual stimuli, whereas over the SPN was larger over occipital areas prior to visual than to auditory stimuli. Similar results were obtained by Ohgami et al. (2004), supporting the assumption that SPN does reflect anticipatory attention.

#### 4. Attention and lateralized difference waves

In order to distinguish subcomponents of the SPN that are related to particular aspects of anticipatory attention, lateralized difference waves have been investigated. In general, the advantage of lateralized difference potentials is that they tend to have circumscribed anatomical sources and well-defined cognitive correlates (Gratton, 1998). All such components, whether designed to study memory, perception, or motor processes, are modeled after the lateralized readiness potential (LRP). To isolate a purely motoric component of the CNV late wave, for example, the LRP is computed by first subtracting waveforms recorded at scalp sites overlying motor cortex on the same side as the cued response from corresponding waveforms at contralateral sites. The resulting difference potentials are then averaged across left- and right-hand response trials (Leuthold et al., 1996).

To extend this technique to the study of visuo-spatial attention, a cue is presented at the beginning of the trial to direct the participant's attention to the left or right half of a computer display. The

EEG waveforms recorded at electrodes ipsilateral to the attended hemifield are subtracted from those at contralateral electrodes, and then left- and right-cue trials are averaged together (Eimer and van Velzen, 2003; Harter et al., 1989). Based on topography, latency and other characteristics a number of lateralized components have been identified. The two that are most relevant toward understanding the SPN are the anterior directing-attention negativity (ADAN) and the late directing-attention positivity (LDAP).

The ADAN typically peaks between 400 and 500 ms after the cue. Its generators have been modeled by paired dipoles that lie within the frontal eye fields (dipole loci:  $x, y, z = \pm 33, -7, 54$  mm; Praamstra et al., 2005; FEF loci:  $x, y, z = \pm 33, -8, 51$  mm; Szczepanski et al., 2010). Identification of the frontal eye fields as sources of ADAN is important because it links this stimulus-preceding negativity to the dorsal attention system, the network responsible for top-down control of goal-directed attention (see Fig. 2, left panel; Corbetta and Shulman, 2002). Consistent with the assumption that ADAN reflects the general control of goal-directed attention, this component has been observed prior to lateralized auditory, tactile and visual task stimuli (Eimer et al., 2002) and prior to cued reaching movements into the attended hemispace by either hand (Gherri et al., 2007).

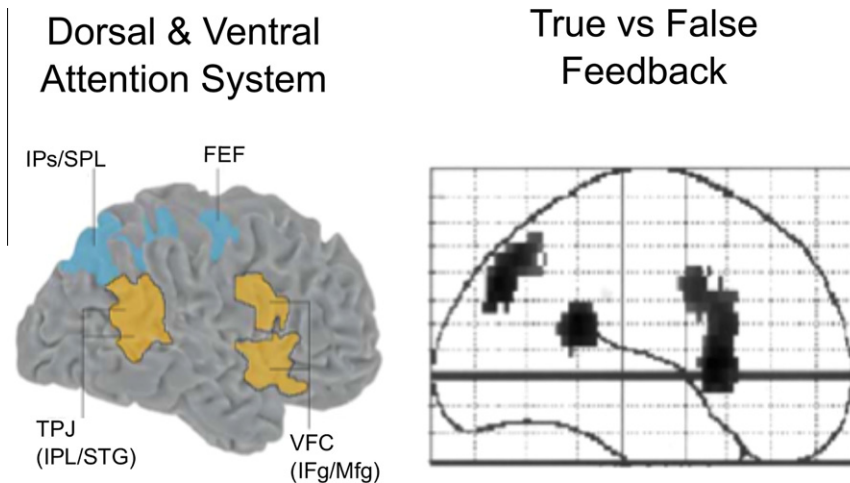
Whether this lateralized component contributes to the pre-feedback SPN presumably depends on the specific task and stimuli that are involved. Using the time estimation task that has become standard in SPN research, Kotani and colleagues (2009) did obtain significant BOLD signal from within the frontal eye fields (34, 18, 48) prior to foveally presented feedback displays.

Also relevant to the SPN is the lateralized directing-attention positivity. The LDAP peaks at around 500–700 ms after the attention-directing cue, and is largest over lateral occipital cortex (Harter et al., 1989; Praamstra et al., 2005). In spite of its occipital maximum, the LDAP is evident preceding tactile and auditory as well as visual stimuli (Eimer et al., 2002). Like the ADAN, it can be observed prior to reaching movements toward the attended hemifield (Gherri et al., 2007).

Based on these properties and on their own dipole modeling results, Praamstra and colleagues (2005) suggested that the LDAP originates not within visual cortex but rather within the "polymodal extrastriate body area" (Astafiev et al., 2004). Relevant fMRI data suggest that LDAP generators are active during the pre-feedback SPN (Kotani et al., 2009). During anticipation of feedback displays in the time estimation task, significant activation was observed at a location (54, -64, 6) close to that of the right hemisphere dipole identified by Praamstra and colleagues (49, -67, -4). However, Kotani and coworkers presented feedback at fixation, as is done in most SPN experiments (but cf. Ohgami et al., 2010). It is not clear how the LDAP, which is recorded during unilateral deployment of attention, would influence the topography and morphology of the SPN prior to centrally displayed feedback.

This highlights the limitations inherent in lateralized difference waves, notwithstanding their anatomical and cognitive specificity. One problem is that by focusing on contralateral-minus-ipsilateral differences the absolute contributions of the two hemispheres are obscured. Does the LDAP, for example, represent greater positivity contralateral to the attended hemispace or more negativity on the ipsilateral side? A second limitation is that by subtracting out non-lateralized potentials, the total size of relevant activity is underestimated. Just as the LRP comprises only the tip of the iceberg with respect to movement-related potentials, the ADAN and LDAP reflect only a small portion of the cortical processes that contribute to the SPN.

Among other processes that one might expect to contribute to the SPN is the control of working memory. In order to make effective use of feedback, the participant needs to remember their



**Fig. 2.** Estimated sources of the stimulus-preceding negativity (SPN) according to an early, positron emission tomography experiment that used a blocked design of true and false feedback (right panel; adapted from Brunia et al. (2000)) as compared with the results of a meta-analysis of previous studies concerning the ventral attention system (left panel, adapted from Corbetta and Shulman (2002)). Abbreviations: FEF, frontal eye fields; IPS, intraparietal sulcus; SPL, superior parietal lobule; TPJ, temporo-parietal junction; IPL, inferior parietal lobule; STG, superior temporal gyrus; VFC, ventral frontal cortex; IFg, inferior frontal gyrus; Mfg, middle frontal gyrus.

previous response, the stimulus that elicited it, and, perhaps, some of the previous action-outcome pairings upon which their expectations are built. Lateralized difference waves are beginning to be used to isolate mnemonic processes such as these. Early research by Ruchkin and colleagues (e.g., Ruchkin et al., 1996; see also Chwilla and Brunia, 1991b) established that a large, bilateral negativity develops during the interval between a briefly displayed memory array and a test probe that must be compared to that array.

To extract a lateralized difference wave from this stimulus-preceding negativity, Vogel and Machizawa (2004) developed a modified paradigm based on visuo-spatial attention. In their paradigm, each trial begins with an arrow at fixation that cues the left or right half of the display as being task-relevant. A to-be-remembered array of geometric figures is then briefly presented on the left and right halves of the screen. After a brief retention interval in which the screen is blank, the bilateral array is displayed again. On half of the trials, one of the items in this test array differs slightly from the memory array (e.g., it is tilted). The subject's task is to indicate whether or not such a change has occurred. Difference waves are computed by subtracting retention-interval waveforms at parietal scalp sites ipsilateral to the cued array from corresponding waveforms at contralateral sites.

The resulting contralateral delay activity, CDA, has been shown to vary in size with the number of items held in visual working memory. With increasing array size, the amplitude of this negative component reaches an asymptote at the subject's memory capacity, as estimated with standardized behavioral measures (Vogel and Machizawa, 2004). The only region of the brain that exhibits this property according to fMRI studies (Todd and Marois, 2004) is the posterior section of the intraparietal sulcus ( $x, y, z = \pm 23, -62, 43$ ). Scalp topography of the CDA is consistent with a source within the intraparietal sulcus (McCollough et al., 2007).

The CDA is reduced in amplitude in people with Parkinson's disease (Lee et al., 2010), which is in agreement with findings for the pre-feedback SPN (Mattox et al., 2006, discussed below). The deficit appears to be caused by impaired selective attention. In comparison with neurologically normal subjects, the participants with Parkinson's disease in Lee et al.'s study were less able to focus attention on relevant items in the cued half of the visual field and hold those items in working memory while they awaited the test array. A related study using fMRI of neurologically intact subjects (McNab and Klingberg, 2008) specifically implicated the basal

ganglia (structures known to be dysfunctional in PD) in the attentional selection of items for storage in working memory.

## 5. Valence and salience

The study of lateralized components such as the CDA and ADAN is a vibrant force in cognitive electrophysiology. However, in order to understand the pre-feedback SPN researchers have shifted their focus toward affective/motivational processes. Part of the empirical rationale for this shift has been the repeated finding that the classical SPN is not observed preceding just any kind of stimulus. For example, either no SPN or only a very small one is found before an instruction stimulus (Damen and Brunia, 1994; Kotani and Aihara, 1999). Furthermore, for visual stimuli presented at fixation, an increase in perceptual difficulty due to stimulus degradation has either no significant effect (Bastiaansen et al., 2002; Hillman et al., 2000) or actually results in a reduced SPN (Kotani and Aihara, 1999).

Another reason for the shift toward affective issues is that it is the ventral rather than dorsal attention system that is most prominent during feedback anticipation. The distinction between two attention networks is based on lesion and neuroimaging research (e.g., Corbetta and Shulman, 2002; Eckert et al., 2008; Fox et al., 2006). The dorsal system implements top-down, goal-driven control of perceptual resources. It is bilateral, comprising mainly the frontal eye fields and intraparietal sulci of the two hemispheres (Fig. 2, left panel). By contrast, the ventral system mediates the involuntary capture of attention by intense, novel, motivationally relevant or otherwise salient stimuli. This network is mainly localized to the ventral frontal cortex and temporo-parietal junction of the right hemisphere. Data from Fox and colleagues (2006) indicate that the temporo-parietal portion of the system extends into the posterior wall of insula. Their data also show that the ventral frontal zone includes the right anterior insula, a structure crucial for awareness of visceral sensations (Craig, 2009).

The ventral attention system has been highly implicated in studies of the SPN's neural generators. In the first such experiment, Böcker et al. (1994) found that most of the variance in SPN amplitude between key press and feedback in the time estimation task was explained by a bilateral fronto-temporal dipole, probably localized in the insular cortex. This suggestion was tested in a

positron emission tomography study by Brunia et al. (2000) in which trial blocks with true and false feedback were compared. These authors found a right-sided activation in ventral prefrontal cortex (~BA45), the junction of the posterior insula with the temporal transverse gyrus, and the posterior parietal cortex (Fig. 2, right panel). The first two regions closely match Corbetta and Shulman's (2002) depiction of the ventral attention system, and the third lies with their dorsal attention network (Fig. 2, left panel). Kotani and colleagues confirmed those results using both blocked and event-related fMRI (Tsukamoto et al., 2006; Kotani et al., 2009, respectively). Their event-related data (Fig. 3) clearly show that, during anticipation of feedback in the time estimation task, motivationally sensitive regions such as the ventral prefrontal cortex and anterior cingulate are active.

Subjective, phenomenological ratings have shown that anticipation of feedback and reward has a hedonic quality that is correlated with anticipatory activation within the reward system (especially, the nucleus accumbens and anterior insula; Knutson and Greer, 2008). Objective psychophysiological methods confirm that the interval during which the SPN is observed has an affective quality. In a study by Hackley et al. (2009), subjects received a reward or punishment 6 s after performance feedback. The reward for correct performance on the pattern discrimination task was a piece of high-quality chocolate; the punishment for committing an error was a segment of bitter-tasting banana peel. During the interval in which food was being anticipated, a brief, but intense burst of white noise was delivered to elicit a startle reflex. The eye-blink component—an index of negative emotional valence—was enhanced prior to the punishment, whereas the post-auricular reflex—an index of positive affect—was larger preceding the reward.

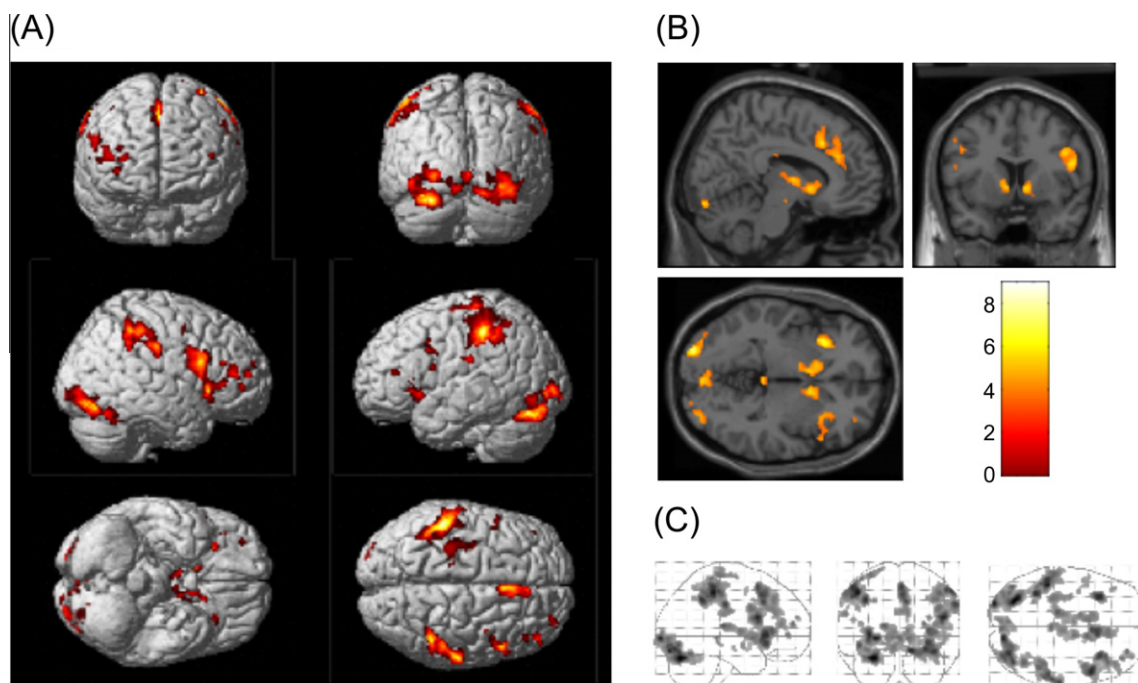
Feedback stimuli are rewarding or punishing because they convey personally relevant information about performance. Negative feedback feels bad and can make one strive to avoid future mistakes. Positive feedback feels good and reinforces the behavior that brought it about; people will work to receive it. If rewards and punishments are contingent on correct and incorrect responses, respectively, the associated SPN amplitudes are considerably larger

than if the incentives are just given gratuitously (Masaki et al., 2010). The SPN is elicited prior to a wide variety of motivationally relevant stimuli. These include evocative photos (Poli et al., 2007), aversive noise (Kotani et al., 2001), monetary rewards (Chwilla and Brunia, 1991a; Kotani et al., 2001, 2003; Masaki et al., 2006, 2010; Ohgami et al., 2004, 2006) and electrical shocks (Babiloni et al., 2007; Böcker et al., 2001).

## 6. The right-hemisphere predominance

The SPNs elicited in these studies exhibited moderate differences in topography. Anticipation of electrical shock produced a fronto-central maximum (Böcker et al., 2001), evocative pictures elicited a broad, fronto-parietal distribution (Poli et al., 2007) and a frontal SPN was observed preceding aversive noise (Kotani et al., 2001). It appears that feedback and other affective/motivational stimuli mainly influence frontal sources of the SPN. Congruent with primary contributions from the ventral attention system, the SPN often shows the right hemisphere preponderance when it precedes feedback, monetary reward, or other affectively salient stimuli. The right hemisphere preponderance is diminished over superior parietal cortex (e.g., Van Boxtel and Böcker, 2004), consistent with the bilateral distribution of the dorsal attention system. Note the symmetry of the parietal activations shown in Fig. 3 in comparison to the ventro-frontal region that includes the anterior insula and frontal operculum (Kotani et al., 2009).

The right-hemisphere predominance for SPN is important because it helps link this component to the ventral attention system. However, it has not always been observed in studies using monetary rewards (Chwilla and Brunia, 1991a; Kotani et al., 2003; Ohgami et al., 2004). Ohgami and colleagues (2006) sought to explain this discrepancy in terms of Davidson and colleagues' (1990) approach-withdrawal theory. This theory maintains that the left frontal lobe is involved in approach behaviors, such as those engaged during appetitive states, whereas right frontal cortex is implicated in withdrawal. Ohgami and coworkers



**Fig. 3.** Event-related functional magnetic resonance imaging (fMRI) of brain activation patterns during anticipation of feedback in the time estimation task. The surface rendered map (a), transaxial section (b), and glass brain views (c) portray activations in the anterior cingulate cortex, the ventral striatum, and the bilateral insular cortex. (Adapted and modified from Kotani et al. (2009)).

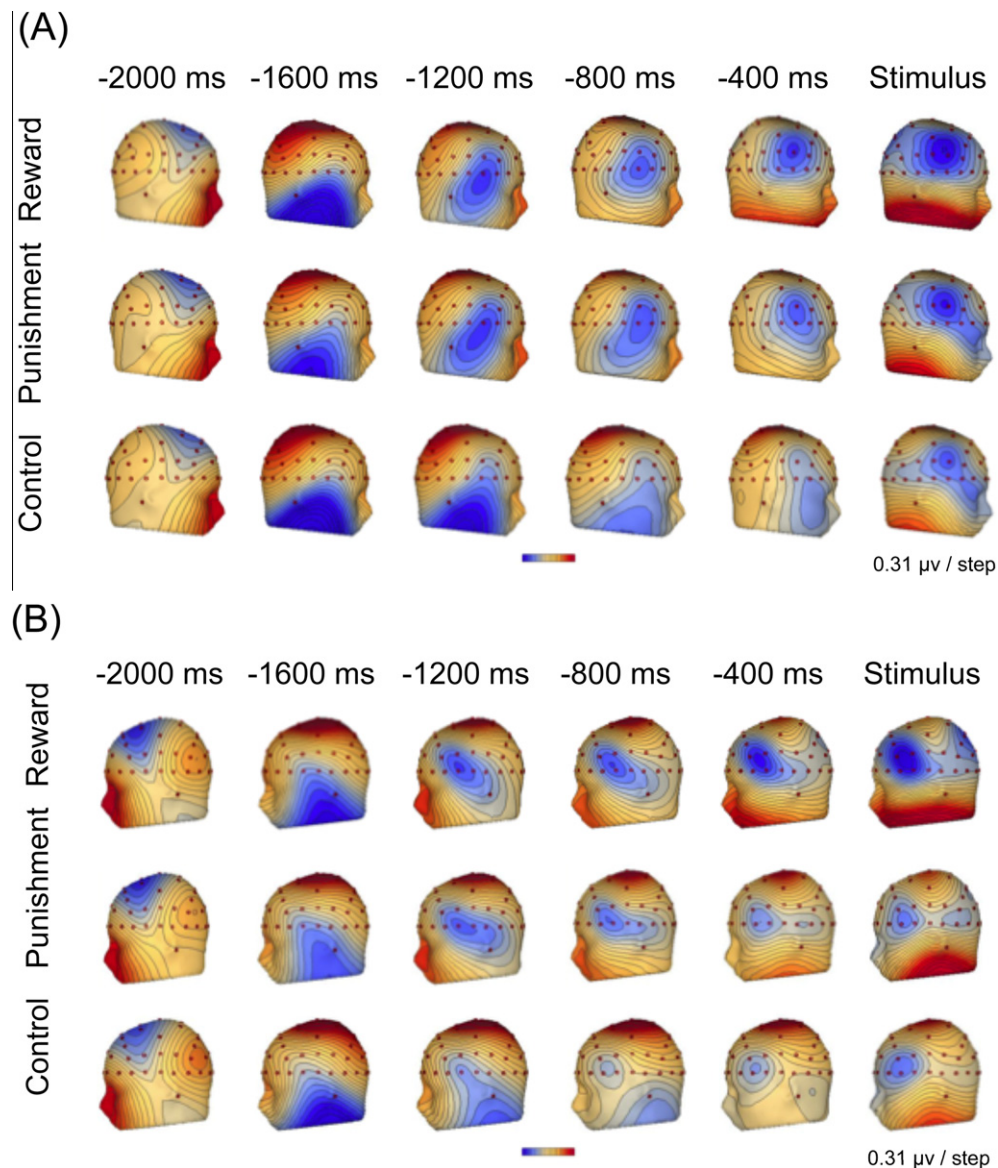
compared reward (monetary gain), punishment (loss), and control (feedback only) conditions using a time estimation task and high density recordings (55 electrodes). They found a significant interaction of monetary manipulation by hemisphere on SPN amplitude (Fig. 4). In the control condition the SPN showed the typical right hemisphere preponderance. In the reward condition, the SPN right hemisphere dominance was eliminated, apparently because of greater left hemisphere activation by appetitive stimulation. In the punishment condition, SPN amplitude tended to be larger at the right hemisphere than at the left hemisphere, but the difference compared with control condition at the right hemisphere was not statistically significant.

Interestingly, the SPN studies using monetary manipulation that could not find the right hemisphere dominance (Chwilla and Brunia, 1991a; Kotani et al., 2003; Ohgami et al., 2004) did not employ punishment conditions but only reward. Anticipation of monetary reward may have activated the left hemisphere, thereby canceling out the inherent right hemisphere preponderance. In the case of studies that employed both reward and punishment

in the same experiment, greater amplitudes over the right hemisphere have generally been obtained (Kotani et al., 2003; Ohgami et al., 2006; Mattox et al., 2006; Masaki et al., 2010).

A review of functional neuroimaging studies of monetary gain and loss by Knutson and Greer (2008) offers mixed support for this interpretation. Congruent with the concept of an inherent right hemisphere bias for the SPN, these authors noted that the right anterior insula is strongly activated during anticipation of either gain or loss. Also consistent with Ohgami and colleagues' explanation was the finding that the right superior frontal gyrus is more activated prior to monetary loss than gain. One study cited by the authors but not included in their meta-analysis (Ernst et al., 2004,) used rewards but not punishments. That study found greater left hemisphere activation relative to control trials lacking monetary incentives, particularly in parietal cortex and the middle frontal gyrus.

In opposition to Ohgami and colleagues' account (and that of Davidson et al., 1990), Knutson and Greer noted that the left superior temporal gyrus was more activated prior to punishment than



**Fig. 4.** (A) Grand average scalp topographies from the right side for Reward, Punishment, and Control conditions of event-related potentials from  $-2000$  ms until stimulus onset. (B) Same, but for the left side. A button was pressed at  $-2000$  ms, and a feedback stimulus was presented at the point labeled "stimulus". A reference-free montage was used. (Adapted and modified from Ohgami et al. (2006).)

rewards and the reverse was true for the right medial frontal gyrus. Reflecting a broader concern with the theory of Davidson and colleagues (1990), it has been suggested that the representation of rewards and punishments is distinguished more along the medial–lateral than left–right dimension (e.g., O’Doherty et al., 2001).

## 7. Dopamine and reward anticipation

Some of the structures identified in Knutson and Greer’s (2008) review as being active during anticipation of reward or punishment are subcortical (i.e., nucleus accumbens, dorsal striatum, amygdala and thalamus). Because the cells comprising subcortical nuclei are not organized in layered, open-field arrangements, it is improbable that these portions of the reward system contribute to the surface-recorded EEG. Their downstream targets within neocortex are more likely to play a role in SPN genesis, and these brain regions been extensively studied by neuroimagers as well as by neurobiologists using invasive techniques. These studies have shown that some orbitofrontal neurons respond selectively during anticipation or receipt of rewarding or aversive stimuli (Thorpe et al., 1983). In this part of the cortex, neurons apparently represent preference and value, forming a key component of networks responsible for motivated, goal-directed behavior (Rolls, 2000).

Orbitofrontal cortex and the closely linked anterior insulae (Öngür and Price, 2000) are well innervated by dopamine secreting cells (Lewis et al., 1988). Based on the seminal work of Schultz and colleagues (e.g., Schultz et al., 2000) it is known that these tegmental neurons fire a phasic burst upon reward receipt that reflects the difference between actual and expected outcome. This is theorized to act as a diffusely broadcast, teaching signal that increases synaptic plasticity (Tsai et al., 2009). As the ability of situational cues to predict response-contingent reward is learned, the discharge of dopaminergic cells advances in time (Schultz et al., 2000). The cells fire in response to the predictive cues (i.e., conditioned stimuli) rather than to the reinforcer itself. This burst is phasic, but the cellular activity in the orbitofrontal regions controlled by dopaminergic neurons is sustained, as is the SPN over prefrontal scalp sites. In humans whose dopamine system has been compromised by mild Parkinson’s disease, the SPN has been found to be reduced in size, especially at higher levels of incentive (i.e., the amount of money won or lost in a pattern classification task; Mattox et al., 2006). In those with advanced Parkinson’s disease, the SPN is completely absent (Hebert et al., submitted for publication).

As mentioned in Section 1, an ERP component that has often been linked to the dopamine reward system is the error-related negativity (ERN). The ERN was initially observed after incorrect responses in choice reaction time tasks, peaking about 80 ms after erroneous responses, and with a fronto-central maximum (Falkenstein et al., 1991). Miltner et al. (1997) showed the occurrence of a similar mediofrontal component peaking about 250 ms after the presentation of feedback that signaled incorrect performance. The same time estimation task that is popular in SPN research was used in that study, and filters were set to a bandpass appropriate for recording slow potentials. Unfortunately, SPN waveforms were not shown, perhaps because the feedback was presented too soon after key press (600 ms) for this component to be clearly distinguished from movement-related potentials.

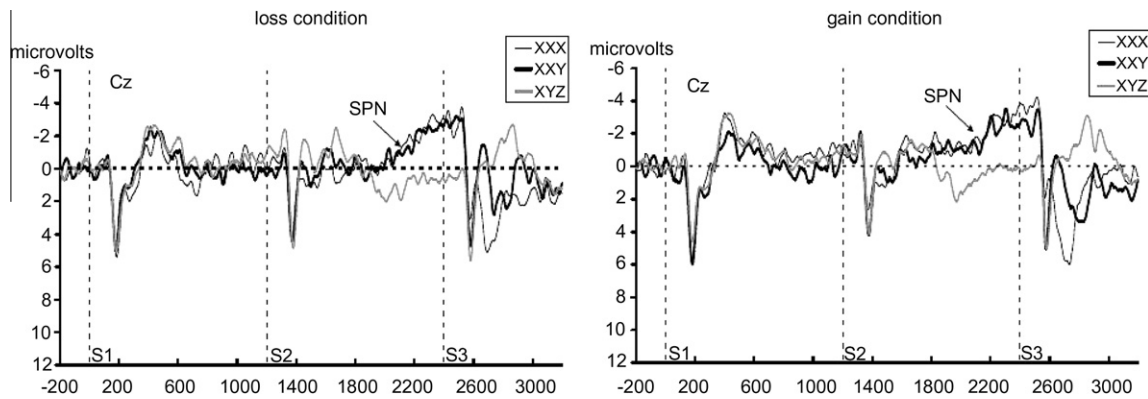
The ERN following performance feedback, also referred to as the feedback-ERN, feedback-related negativity (FRN), or mediofrontal negativity (MFN), was originally conceived of as reflecting an error detection system just like the regular ERN (Miltner et al., 1997). This was later replaced by a conflict monitoring account, because ERN research suggested that the negativity could sometimes also be elicited in the absence of overt errors (Cohen et al., 2000). Holroyd and Coles (2002) hypothesized that the FRN reflects a

negative reward prediction error system, driven by dopamine, that is called into action when it is first detected that the consequences of an action are worse than expected. Their theory has become known as the reinforcement learning theory. Similarly, Gehring and Willoughby (2002) found the FRN to be elicited in a gambling task when the stimulus indicated a monetary loss, even when the participants made a correct choice by avoiding a worse loss.

There are two salient features in FRN research that are important for the current review. First, most research somehow involves a response. This probably relates to the overarching research theme of performance monitoring. Responses have to be issued in order for monitoring to take place, and rewards or punishments should be contingent upon recent action for learning to take place. The limiting issue, however, is that responses are very much coupled to the neurotransmitter dopamine and activity of the basal ganglia, just as the performance monitoring/reward anticipation system that we are trying to study. Although the SPN is larger when rewards are contingent on prior action than when they are given gratuitously (Masaki et al., 2010), it would be useful to study motivational processes in isolation. Second, with only few exceptions (e.g., Masaki et al., 2006), FRN investigators only analyze their ERP data *after* the feedback, because that is when the FRN occurs, and thus do not report on the SPN that precedes it. We believe this to be a missed opportunity, because the tasks that are used easily allow for the measurement of the SPN. All researchers have to do is apply a wider filtering bandwidth and extend the time from key press to feedback enough for movement-related potentials to dissipate.

A study that attempted to remedy these issues is reported by Donkers et al. (2005). They used a ‘slot machine’ task in which participants were shown a succession of three digits that they were to observe passively. There was no motor response required. Participants were only told that three identical digits would result in monetary gain (or loss, according to the condition). The information value of each anticipated digit depended on what had already occurred. Donkers and colleagues found that stimuli that averted a gain or a loss were always followed by the FRN, and preceded *but not followed* by the SPN (see Fig. 5). Thus, in a sequence of three identical digits (XXX, which would result in a gain or a loss), all stimuli were preceded by an SPN. The SPN increased in amplitude toward the end of the sequence, and no FRN was observed. When the last stimulus deviated (XXY), all three stimuli were preceded by the SPN, and the last one was followed by the FRN. When the second stimulus deviated from the first (XYZ), that second stimulus was preceded by the SPN and followed by the FRN, and the third stimulus was not preceded by the SPN. These data nicely show the interplay between the reward prediction system (measured by the SPN), and the reward prediction error system (measured by the FRN).

Studies of patient groups with dopaminergic disorders support the contention that SPN and FRN are complementary indices of the reward system. Already mentioned are the findings that the SPN is reduced in mild Parkinson’s disease (Mattox et al., 2006), and is completely absent in severe Parkinson’s disease (Hebert et al., submitted for publication). Similarly, fMRI studies by Knutson and colleagues (e.g., Juckel et al., 2006) have shown that reward anticipation processes within the ventral striatum is grossly abnormal in people with schizophrenia (e.g., Juckel et al., 2006). With regard to post-feedback processes, schizophrenic patients show reduced FRN amplitudes (Morris et al., 2008) as do monkeys that have been administered dopamine antagonists (Vezoli and Procyk, 2009). The FRN has not been assessed in people with Parkinson’s disease, but the closely related ERN has sometimes been found to be diminished in this population (e.g., Falkenstein et al., 2001). The ERN has also found to be attenuated in major depression (e.g., Ruchow et al., 2006), as is the FRN (Foti and Hajcak, 2009).



**Fig. 5.** Feedback-related negativity (FRN) and stimulus-preceding negativity (SPN) recorded in the slot machine task, as discussed in the text. (Adapted from Donkers et al. (2005).)

### 8. The brain region to integrate SPN studies: insular cortex

As mentioned above, the SPN was first isolated during attempts to identify non-motoric components of the CNV. Since then, various kinds of experimental factors have been manipulated in order to reveal the functional significance of the SPN: the type of anticipated information, stimulus modality, stimulus salience, and monetary reward and punishment. Although these findings are quite diverse, an integrating principle can be found in a hypothesis originally offered by Böcker and coworkers (1994). Based on dipole modeling of scalp topographic data, these authors hypothesized that insular cortex is one of the main sources of the SPN.

The functions of the human insular cortex was poorly understood at the time Böcker and coworkers presented their idea, but this region has recently been the focus of a number of functional neuroimaging studies (e.g., Eckert et al., 2009; Taylor et al., 2009; Nelson et al., 2010). For example, Critchley (2005) reviewed the literature and concluded that activation in the insular cortex, especially the right anterior insula, is the best candidate for representation of visceral sensations in Bechara and Damasio's (2005) well-known somatic marker hypothesis. The hypothesis assumes that when an emotional stimulus evokes somatic states such as increasing heart rate, this state is represented in the somatosensory cortices, including the SI, SII and the anterior insula. These somatic patterns can then be re-activated by memories or by imagined, future scenarios. Such "gut feelings" bias or guide our behavior, especially in situations that require rapid decisions or are too complex to think through analytically.

Other theorists (e.g., Nelson et al. 2010) have proposed that insular cortex plays an important role in focal attention and task level control. Of particular relevance toward understanding the SPN is a review by Eckert and colleagues (2009). These authors suggest that the right anterior insula modulates the excitability of the dorsal attention system, thereby serving as the interface between the ventral and dorsal networks. Assuming that the right anterior insula is involved in both awareness of interoception and control of attention, it could play the role of monitoring deviations from homeostasis, bringing these deviations into awareness and engaging attention within the dorsal system. This would then lead to goal-directed behaviors capable of normalizing homeostasis.

Because it comprises a portion of the reward system, the insula is also involved in addiction. Naqvi and Bechara (2009) argue, for example, that the insula has a role in the generation of conscious feeling of drug urge. Naqvi and coworkers (Naqvi et al. 2007) compared smokers who sustained damage in the insula with smokers who suffered lesions in other brain regions. They found that smokers with insular lesions exhibited a remarkable ability to quit smoking easily, immediately, without relapse, and without

persistence of the urge to smoke. The fact that the anterior insula receives dopaminergic innervation (Gaspar et al. 1989) and has a high density of D1 dopamine receptors (Hurd et al. 2001) also supports the involvement of the insula in addiction. Finally, the strong functional connectivity that has been documented between the insula and cingulum (Taylor et al., 2009; Nelson et al. 2010) is further evidence for a tight linkage between the SPN, which originates partly in the insula, and the FRN, which is generated mainly by the anterior cingulate.

### 9. Conclusions and future directions

The stimulus-preceding negativity comprises a family of ERPs that are concerned with attentional control. Careful comparisons of dipole modeling and functional neuroimaging data have begun to reveal the patterns of underlying generators in a few, well studied, experimental paradigms. For example, portions of the dorsal attention network, such as the frontal eye fields and intraparietal sulcus, are recruited when one deliberately prepares to perceptually discriminate a lateralized task stimulus. By contrast, when a person anticipates receiving a stimulus of immediate motivational relevance such as an electric shock or a monetary reward, portions of the ventral attention network are recruited. The right anterior insula and overlying frontal operculum is particularly important in this regard, as is the cortical area in or just above the temporo-parietal junction.

The anticipation of motivationally relevant stimuli plays a critical role in two prominent theories that have attempted to bridge the disparate fields of affective and cognitive neuroscience. According to the temporal difference model of Schultz and colleagues (1997, 2000), the dopaminergic reward system broadcasts a teaching signal when the consequence of an action is better than expected. The SPN provides a temporally precise index of neocortical processes underlying that expectation. According to the somatic marker theory (Bechara and Damasio, 2005), when a person imagines the consequences of an action he or she might make, a "gut feeling" is generated that helps guide decision making. The SPN provides a surface electrophysiological index of anticipatory activity within the most likely site (Craig, 2009) for that gut feeling, the right anterior insula.

Future research should be able to capitalize on the diverse experimental paradigms that have been developed by neurobiologists, fMRI researchers, and ERN/FRN psychophysicists who study reward expectation. By employing a wide recording band-pass and delayed pre-feedback intervals, it is possible to assess FRN and SPN in the same experiment (Masaki et al., 2006; Donkers et al., 2005). Perhaps most critically, researchers need to develop

cost-effective methods for distinguishing contributions to the scalp-recorded SPN of motivationally versus perceptually relevant generators. It would be inefficient to incorporate a manipulation of reward size (Mattox et al., 2006) or visuo-spatial feedback location (Ohgami et al., 2010) into every experiment. Factor analytic methods such as Independent Component Analysis might accomplish this goal, if adequate anatomical markers can be identified.

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