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Research Report

Affective-motivational influences on feedback-related ERPs in a gambling task

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MFN, medial–frontal negativity
ACC, anterior cingulate cortex
SPN, stimulus-preceding negativity

ABSTRACT

Theories have proposed that both the stimulus-preceding negativity (SPN) and the medial frontal negativity (MFN) reflect affective/motivational processing. We examined the effect of the motivational impact of feedback stimuli on these ERPs using a simple gambling task, focusing on the influence of prior losses and gains on ERPs and choice behavior. Choices were riskier following large losses than following small losses or large gains. The MFN, however, was larger following larger gains. The SPN preceding the outcome was also larger after a greater gain. Thus, we confirmed that both the MFN and the SPN respond to the motivational properties of the feedback. A dissociation between risk-taking behavior and these ERPs suggests that there could be two monitoring systems: one that leads to riskier responses following losses and a second that leads to heightened expectancy.

1. Introduction

The rapid evaluation of response outcomes and the anticipation of future events are important for enabling humans to guide subsequent choices to avoid other negative events. Recent event-related potential (ERP) studies have reported neurophysiological activity that is involved in rapidly evaluating the motivational significance of ongoing events. A number of these studies have focused on a medial–frontal negativity (MFN) elicited by reward feedback in simple learning and gambling tasks (e.g., Gehring and Willoughby, 2002, 2004; Holroyd and Coles, 2002; Miltner et al., 1997; Yeung and Sanfey, 2004). The MFN in these studies is a negative-going deflection in the ERP that has a frontocentral distribution, most likely reflecting neural activity generated in the anterior cingulate cortex (ACC). Functionally, it appears to reflect a process involved in evaluating the motivational significance of ongoing events (Gehring and Willoughby, 2002; Holroyd and Coles, 2002). It peaks approximately 250 to 300 ms following a signal conveying feedback about the

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incorrectness of a response or about a monetary loss (for a review see Nieuwenhuis et al., 2004b).[1]

Gehring and Willoughby (2002) hypothesized that the process reflected by the MFN was involved in quickly determining the motivational impact of ongoing events. A related but more specific hypothesis was offered by Holroyd and Coles (2002), who suggested that MFN activity (or the "feedback ERN") is elicited when an error processing system detects events that are worse than expected. Gehring and Willoughby (2002) reported that losses evoked MFN activity even when the loss was the most advantageous outcome on a trial, suggesting that the MFN responded to the gain/loss status of the event rather than to the indication that one response was correct and the other was not. Their data also suggested that the MFN elicited by a monetary loss was also influenced by the motivational impact of previous bad outcomes, because a monetary loss affected the risk-taking behavior and MFN on subsequent trials. Other studies also indicate a strong influence of context on the MFN elicited by losses and negative events (Holroyd et al., 2004).

A fundamental question concerning the factors that influence the MFN is whether there is a potential effect of anticipating the outcome (i.e., expectancy) that is distinct from the monetary value associated with that outcome. The response to losses could occur because of the negative utility (value) associated with the outcome, but it could also occur because the subject, choosing a gamble, chose the alternative that seemed most likely to result in a gain. The loss is thus not only a negative event, but also, potentially, an unexpected one. In many of the tasks that have elicited the feedback-related MFN (Gehring and Willoughby, 2002; Holroyd and Coles, 2002; Miltner et al., 1997), negative and positive outcomes have been equiprobable. That the probabilities were equal does not rule out the possibility that at some level the chosen outcome was seen as more likely than the unchosen one to result in a gain. Likewise, risk-taking behavior could be driven either by the perceived value of a gamble or the perceived probability of a gain.

One way to dissociate anticipatory and evaluative processing would be to record ERPs in the period between the choice and the appearance of the outcome. In the present study, we explored the anticipation of outcomes by recording the stimulus-preceding negativity (SPN) during the waiting period prior to the outcome (Brunia, 1988; Brunia and Damen, 1988). Brunia and his colleagues have identified negative slow brain potentials that precede the occurrence of predictable events. The SPN is the non-motoric component of the late contingent negative variation (CNV) (Walter et al., 1964), which is distinct from the motoric component, the readiness potential (Kornhuber and Deecke, 1965). Feedback stimuli normally used in the SPN paradigm provide the participant with knowledge of results. This SPN shows a right hemisphere preponderance of negativity and largest amplitudes over the parietal cortex (Brunia and van Boxtel, 2001) and is referred to as the pre-knowledge-of-results SPN (Brunia, 1988). Although other types of SPN have been identified (Böcker et al., 2001; van Boxtel and Böcker, 2004), the paradigm used in the current study should only produce a pre-knowledge-of-results SPN, therefore for brevity, we shall refer to it simply as SPN.

According to a thalamic gating model (Brunia, 1999), the SPN is a manifestation of anticipatory attention. Recent studies have reported that the SPN represents anticipation of the affective-motivational valence of feedback stimuli as well as their informative value. The SPN shows the largest amplitudes during anticipation of stimuli with emotional valence (Böcker et al., 1994, 2001; Donkers and van Boxtel, 2005). Emotional valence comprises affective valence that gives rise to appraisal and motivational valence that directs behavior (Böcker et al., 2001).

Although the stimuli in most studies that showed the SPN were aversive, increased non-motoric negativity was also reported by studies that used stimuli with positive valence, such as nude slides (e.g., Howard et al., 1992; Simons et al., 1979). In addition, the SPN increased with monetary reward in a time estimation task (Kotani and Aihara, 1999). Thus, factors that induce affective arousal – both positive and negative – might be critical for development of the SPN. These previous findings suggest that the amplitude of the SPN should be sensitive to the motivational incentives delivered by outcome stimuli.

Interestingly, in previous reports, a symmetrically frontocentral SPN, consistent with involvement of the ACC, was observed before stimuli that involved negative affect (e.g., fear slides) (Böcker et al., 2001), whereas a right-lateralized frontocentral SPN, possibly due to activity of the insular cortex, was observed before stimuli with motivational valence (e.g., monetary reward and punishment) (Kotani and Aihara, 1999). Using a spatiotemporal dipole analysis, Böcker et al. (2001) also found involvement of insular cortex in the SPN. Böcker et al. (2001) suggested that the ACC is more involved in the SPN related to negative affect, whereas the insular cortex is more involved when there is motivational (incentive) information conveyed by the feedback signal. This line of reasoning suggests that the SPN preceding motivational feedback would show a right-lateralized frontocentral distribution, whereas the SPN related to negative affect would show more symmetrical negativity over frontocentral regions.

Because both the MFN and the SPN might represent affective-motivational processing, one could hypothesize that they would respond similarly to the motivational impact of the previous outcome and that they would both vary with the probability of risk-taking behavior. On the other hand, it is also possible that risk-taking behavior would be independent of the motivational state reflected by the SPN, in which case the SPN would not vary with the probability of a risky choice.

[1] Authors have referred to this deflection in the ERP waveform as the error-related negativity (feedback ERN; e.g., Holroyd and Coles, 2002). Others refer to it as the feedback-related negativity. We use the term medial–frontal negativity here as a generic term to describe its scalp distribution and polarity. The relationship between this feedback-related MFN and the response ERN is currently an active area of investigation. The more anterior and right-lateralized topography of the feedback-related MFN suggests that there must be a difference in the configuration of generators that gives rise to the two components, although one of these neural generators may be active in both cases (Gehring and Willoughby, 2002, 2004; Holroyd and Coles, 2002).

Thus, we focused on testing whether the processing associated with risk-taking in a simple gambling task depends on the motivational impact of the previous outcome or on the affective-motivational state induced by the current choice, or both, using the SPN and the MFN.[2] First, we tried to replicate the findings of Gehring and Willoughby (2002) that the MFN represents processing of monetary losses rather than the detection of choice errors and that the MFN becomes larger as a function of preceding outcomes (i.e., the larger the monetary loss on the previous trial, the larger the MFN elicited by a monetary loss on the current trial), which would link the MFN to the probability of risk-taking behavior. Second, we tested the hypothesis that the MFN, the SPN, and risky choice behavior would all be similarly affected by the motivational impact of the previous outcome: after bigger monetary losses they should be largest and after bigger monetary gains they should be smallest (Gehring and Willoughby, 2002). Alternative scenarios are possible, however, in which the two components do not show the same relationship to the previous outcome and to risk-taking behavior.

2. Results

2.1. Behavioral results

The mean monetary gain was 385 yen (SD = 674). Fifteen participants gained money at the end of the experiment. The best score was a gain of 1560 yen and the worst was a loss of 1140 yen.

Table 1 shows the mean probability of a risky choice in each outcome condition. The participants tended to make risky choices (i.e., choosing 50 yen rather than 10 yen) on trials following losses of 50 yen. On the other hand, they did not make risky choices after gains of 50 yen. This result is similar to the finding of Gehring and Willoughby (2002), whose results showed a strong linear relationship between previous outcome and riskiness of choices. We also found a linear relationship between the riskiness of the choice and the value of the preceding outcome ($F(1,19) = 12.78$, $P = 0.002$). A one-way ANOVA revealed a significantly higher probability of a risky choice after Loss 50 than after Gain 50 and Loss 10 ($F(3,57) = 5.43$, $P < 0.01$, post hoc test: $Ps < 0.05$) and a trend of a higher probability following Loss 50 relative to Gain 10 ($P = 0.07$). In addition, there was a trend of a higher probability of a risky choice after Gain 10 relative to Gain 50 ($P = 0.08$). Table 1 also shows reaction time (RT) for choice responses in each previous outcome and control condition. A one-way ANOVA including the control condition revealed longer RTs for the control than for the other conditions ($F(4,76) = 17.46$, $\varepsilon = 0.28$, $P < 0.001$; post hoc, $Ps < 0.001$), but no differences were observed across the previous outcome conditions.

Table 1 – The effect of the preceding outcome on the riskiness of behavior with the standard error of the mean in parentheses

Preceding outcome	Risky choice (%)	Reaction time (ms)
Gain 50	39.6 (3.6)	622 (34.0)
Gain 10	47.4 (3.2)	613 (33.9)
Loss 10	48.0 (2.2)	602 (33.6)
Loss 50	57.1 (3.4)	615 (35.2)
Control		788 (40.2)

Mean reaction times are calculated by pooling Current choice 50 and Current choice 10. Note that the participants did not choose between the monetary options in the control condition, so that risky choice is not reported.

To explore the effects of preceding outcomes on riskiness of behavior further, we computed mean probability of a risky choice according to the number of successive preceding gains or losses. A 3 (sequence length: 3, 2, or 1) × 2 (sequence type: Gain/Loss) repeated measures ANOVA revealed a main effect of sequence type, indicating a greater proportion of risky choices following successive losses (53.5%) than following successive gains (42.9%) ($F(1,19) = 10.97$, $P < 0.005$). A main effect of sequence length was also significant ($F(2,38) = 3.57$, $\varepsilon = 0.83$, $P < 0.05$). Post hoc tests revealed riskier choices after sequences of length three than after sequences of length two ($P < 0.05$) (1st trial: 47.6%, 2nd: 46.7%, and 3rd: 50.2%). In addition, an interaction of sequence type by sequence length was significant ($F(2,38) = 10.19$, $\varepsilon = 0.75$, $P < 0.005$) (Table 2). Post hoc tests revealed that following successive losses the probability of a risky choice increased with the sequence length (1 loss vs. 2 losses: $P < 0.05$; 2 losses vs. 3 losses: $P = 0.06$). Following successive gains, risky choices were less probable after 2 successive gains than after 1 gain ($P < 0.005$), but there was no difference between 2 and 3 successive gains. The probability of a risky choice following gain sequences differed from that following loss sequences after sequences of length two ($t(19) = 3.54$, $P < 0.005$) and after sequences of length three ($t(19) = 3.64$, $P < 0.005$).

2.2. The MFN

Fig. 1a shows grand-averaged ERP waveforms at FCz and scalp topography of the difference wave obtained by subtracting the ERPs on the gain trials from those on the loss trials. As can be seen in the figure, the frontocentrally distributed MFN peaking at about 250 ms was exclusively elicited by the feedback signal that informed the participants of a monetary loss. The negativity is also slightly lateralized to the right, consistent with the topography reported by Gehring and Willoughby (2004).

Fig. 1b (left panel) shows the grand-averaged ERPs at FCz elicited by feedback signals based on the larger subset of trials showing all combinations of correctness and outcome (i.e.,

[2] An anonymous reviewer suggested that variation in the MFN or SPN associated with previous outcomes might reflect representations of the outcomes in memory rather than their motivational impact. The effects reported in earlier studies and those we report here, however, depend on the valence and magnitude of the previous outcomes. An explanation based on memory representations alone would have to postulate that the representations are specifically reward-related (rather than being value-neutral representations of sequence length or some other aspect of the past outcomes). It then becomes difficult to tease the motivational and memory-based explanations apart, because the motivational changes induced by previous outcomes should be tightly linked to memory representations of the outcomes' reward properties.

Table 2 – The effect of the number of successive preceding gains or losses on the probability of a risky choice and on SPN amplitude with the standard error of the mean in parentheses

Sequence of preceding outcomes	Risky choice (%)	SPN (μV)
Gains		
1	47.8 (2.3)	−2.61 (0.41)
2	39.5 (2.7)	−1.72 (0.44)
3	41.3 (3.1)	−1.68 (0.62)
Losses		
1	47.5 (1.9)	−1.38 (0.46)
2	53.9 (2.5)	−2.28 (0.56)
3	59.1 (3.6)	−2.22 (0.50)

Table 3 – Mean MFN amplitudes (μV) at FCz with standard error of the mean in parentheses for the Gain/Loss status and for the Correct/Error status

	All conditions	Critical conditions (4)
Gain/correct choice	8.16 (0.73)	6.19 (0.63)
Gain/error	7.76 (0.86)	7.76 (0.86)
Loss/correct choice	5.88 (0.59)	5.88 (0.60)
Loss/error	6.09 (0.58)	5.00 (0.55)

ERPs for four conditions based on all conditions shown in Table 5 (all conditions) and based on only the four conditions, as indicated in Table 5 (critical conditions).

Loss/Error, Loss/Correct, Gain/Error, and Gain/Correct) and right panel shows the ERPs derived from the 4 conditions chosen by Nieuwenhuis et al. (2004a).

We carried out a 2 (Outcome: Gain/Loss) × 2 (Correctness: Correct/Error) repeated measures ANOVA for the MFN amplitude measure at FCz (Table 3). There was a significant main effect of Outcome ($F(1,19) = 30.43$, $P < 0.00005$), but no effect of Correctness for the conditions shown in the left panel of Fig. 1b. However, the ANOVA revealed an interaction between Outcome and Correctness in the analysis shown in the right panel of Fig. 1b ($F(1,19) = 15.62$, $P < 0.005$). Loss trials showed greater negativity than gain trials only for error outcomes ($P < 0.01$), not for correct outcomes.

Fig. 2 depicts the MFNs at FCz, quantified from the loss–gain difference waveform and averaged according to the outcome on the previous trial. A 4 (Previous outcome: Gain 50/Gain 10/Loss 50/Loss 10) × 2 (Current choice: 10/50) repeated measures ANOVA revealed a significant interaction of Previous outcome × Current choice ($F(3,57) = 4.19$, $\varepsilon = 0.79$, $P < 0.05$), indicating that following a monetary gain (previous outcome Gain 50/Gain10), the MFN was larger when the current outcome was 50 Yen than when it was 10 Yen (at previous-outcome Gain 50: $t(19) = 3.34$, $P < 0.01$, at Gain 10: $t(19) = 2.92$, $P < 0.01$), and the MFN was larger after Gain 50 than after Loss 50 for Current choice 50. A repeated measures ANOVA analyzing the effect previous outcome on Current choice 50 trials showed a significant main effect of previous outcome, $F(3,57) = 3.20$, $\varepsilon = 0.84$ $P < 0.05$; post hoc test: Gain 50 vs. Loss 50: $P < 0.05$) (Fig. 3).

2.3. The SPN

Fig. 4 shows the grand-averaged SPNs for the 50 current choice, the 10 current choice, and the control conditions. SPNs for both the 50 and 10 choices developed gradually over centroparietal regions and showed a prominent negativity especially 1 s before the feedback signal, which is revealed by a visual inspection of waveforms comparing waveforms in the choice conditions with that of the control task.

A 2 (Current choice: 10/50) × 5 (Caudality: Frontal/Central/Parietal/Temporal/Occipital) × 2 (Hemisphere: Right/Left) three-way repeated measures ANOVA was carried out on the subtracted SPN amplitudes. The effect of Caudality was significant ($F(4,76) = 6.39$, $\varepsilon = 0.52$, $P < 0.005$). The SPN was larger over central, parietal, and occipital regions than over

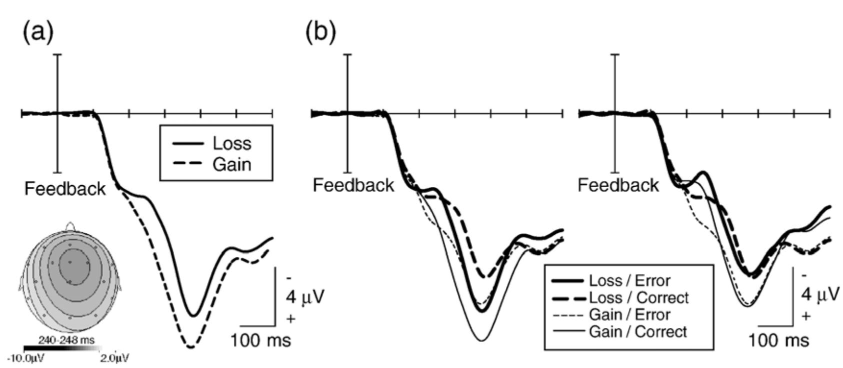

Fig. 1 – (a) ERP waveforms at FCz and the scalp topography of the difference wave obtained by subtracting the ERPs on all gain trials from those on all loss trials. (b) The grand-averaged feedback-related ERPs separately averaged for each case (i.e., Loss/Error, Loss/Correct, Gain/Error, and Gain/Correct). Left panel shows the ERPs for the four conditions derived from 12 possible combinations and right panel shows the ERPs for the 4 conditions chosen by Nieuwenhuis et al. (Kotani et al., 2003).

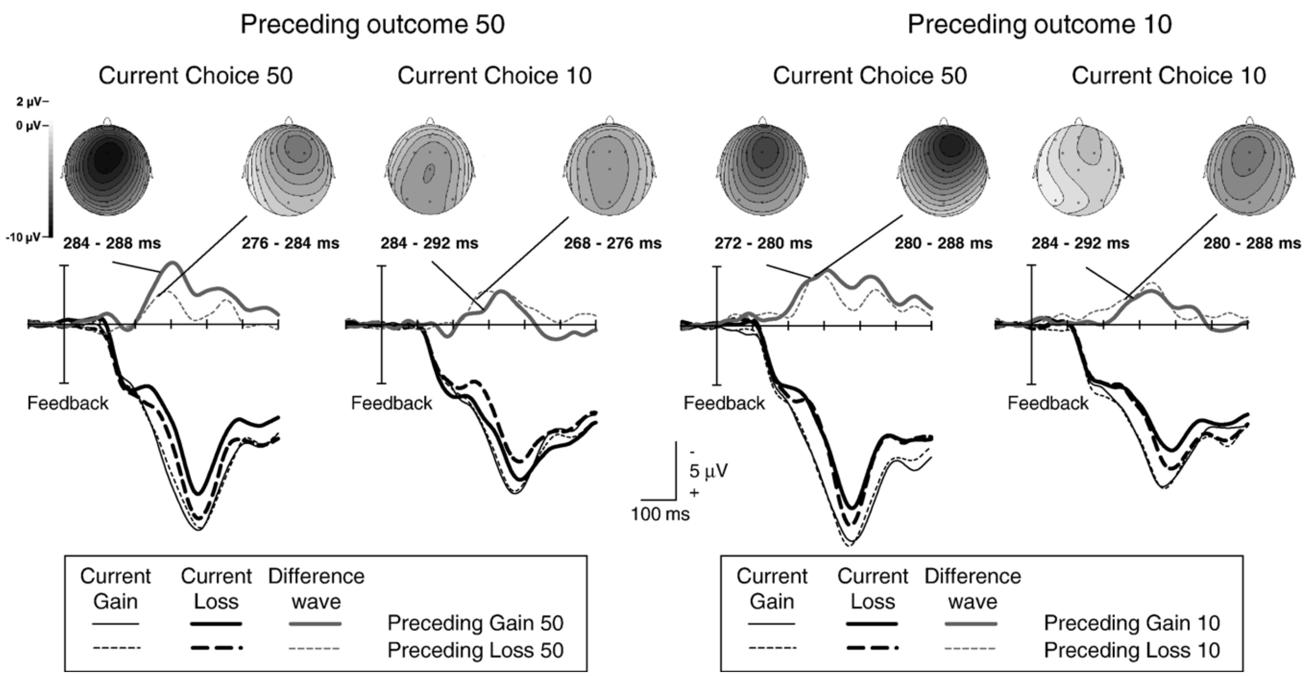

Fig. 2 – The grand-averaged MFNs and the difference waves (loss minus gain) for each previous outcome. The topographical maps of the difference waves were drawn based on amplitude values taken at the mean peak latency of the MFN in each condition.

frontal regions (Ps < 0.005), and the SPN over temporal regions was marginally larger than over frontal regions ($P < 0.08$) and marginally smaller than over parietal ($P < 0.09$) and occipital regions ($P < 0.06$).

Because choice behavior and the MFN were both affected by the outcome on the previous trial, we also averaged the SPN according to previous outcomes. Fig. 5 shows the SPNs for each previous outcome, following subtraction of the control task waveform, and it also shows the topographical distribution of SPN following Gain 50 trials, for both Current choice 50 and 10 (top). On trials where the subject chose 50, examination of the waveforms suggests that the SPN became larger as a function of the previous outcome in the order of Loss 50 < Loss 10 < Gain 10 < Gain 50. In contrast, on trials where the subject chose 10, the SPN became larger in the order of Loss 10 < Gain 10 < Loss 50 < Gain 50.

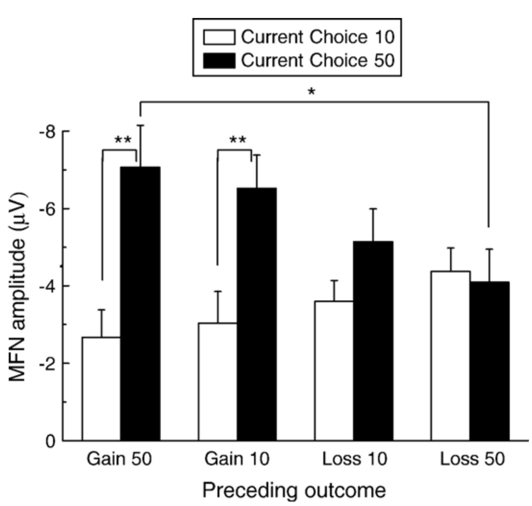

Fig. 3 – Mean MFN amplitude (μV) at FCz for each preceding outcome condition. $^{**}P < 0.01$, $^{*}P < 0.05$.

We carried out a 2 (Current choice: 10/50) × 4 (Preceding outcome: Gain 10/Gain 50/Loss 10/Loss 50) × 5 (Caudality: Frontal/Central/Parietal/Temporal/Occipital) × 2 (Hemisphere: Right/Left) repeated measures ANOVA on the mean amplitude measure computed over the 200 ms epoch preceding the feedback signal. It revealed an effect of Preceding outcome ($F(3,57) = 3.55$, $\varepsilon = 0.69$, $P < 0.05$). The SPN was larger following Gain 50 than following other outcomes (Ps < 0.05). The effect of Caudality was also significant ($F(4,76) = 6.36$, $\varepsilon = 0.49$, $P < 0.005$). The SPN was larger over central, parietal, and occipital regions than over frontal regions (Ps < 0.05), and the SPN over temporal regions was marginally larger than over frontal regions ($P = 0.07$) and marginally smaller than over central regions ($P = 0.07$). A significant interaction of Caudality × Preceding outcome was revealed ($F(12,228) = 2.42$, $\varepsilon = 0.42$, $P < 0.05$). A post hoc test showed that the SPN was larger following Gain 50 outcomes than following other outcomes at frontocentral electrode sites (simple effect of Previous outcome at frontal: $F(3,57) = 5.32$, $\varepsilon = 0.79$, $P < 0.01$; central: $F(3,57) = 3.70$, $\varepsilon = 0.67$, $P < 0.05$) (Table 4). This effect also existed at temporal electrode sites ($F(3,57) = 2.61$, $\varepsilon = 0.80$, $P = 0.08$). In addition, the interaction of Caudality × Hemisphere was marginally significant ($F(4,76) = 2.96$, $\varepsilon = 0.49$, $P < 0.07$). The interaction of Current choice × Preceding outcome was marginally significant ($F(3,57) = 2.64$, $\varepsilon = 0.78$, $P < 0.08$). Examination of the waveforms suggests that on Current choice 50 trials, the effects of the different levels of prior outcome were more distinguishable than on Current choice 10 trials.

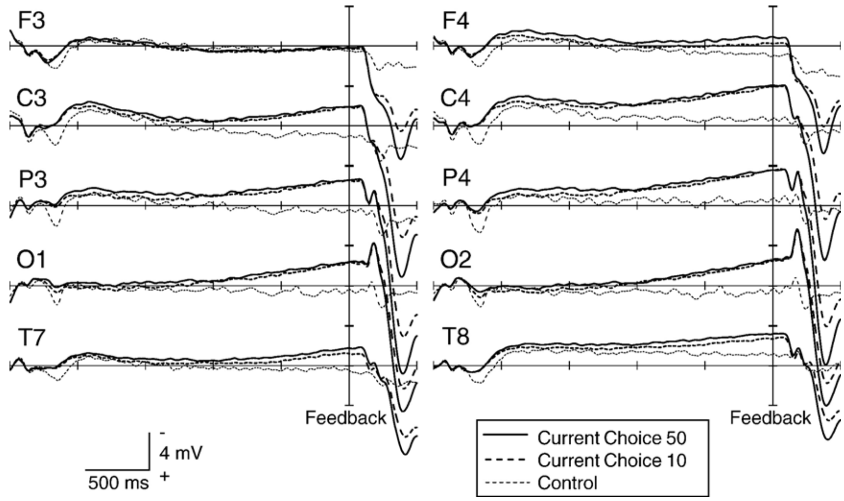

Fig. 4 – The grand-averaged SPNs for the 50 choice, 10 choice, and control conditions. The SPNs are depicted from the response onset, 2.5 s preceding the feedback signal.

To explore the effects of preceding outcomes further, we computed SPN averages according to the number of successive preceding gains or losses. Fig. 6 depicts the SPN at C4 (where it was largest, see Fig. 5) averaged according to the number of preceding gain or loss outcomes 3 (sequence length: 3, 2, or 1) × 2 (sequence type: Gain/Loss) × 5 (Caudality) × 2 (Hemisphere) repeated measures ANOVA revealing a significant interaction of Gain/Loss type by sequence length ($F(2,38) = 8.59$, $\varepsilon = 0.99$, $P < 0.005$) (Table 2). Post hoc tests indicated that the SPN was significantly larger after three Losses and two Losses than after one Loss (an ANOVA restricted to loss trials showed a main effect of sequence length: $F(2,38) = 4.58$, $\varepsilon = 0.91$, $P < 0.05$; three and two Losses > one Loss: $Ps < 0.05$). For Gains, the main effect of preceding outcome was marginally significant, $F(2,38) = 3.27$, $\varepsilon = 0.81$, $P = 0.05$. Post hoc analyses indicated that compared to one Gain, there were smaller SPNs after two Gains ($P < 0.05$) and a trend toward smaller SPNs after three Gains ($P < 0.08$). The significant Gain/Loss × Caudality ($F(4,76) = 2.79$, $\varepsilon = 0.76$, $P < 0.05$) interaction indicated a disappearance of the amplitude difference between frontal and temporal regions after gain sequences (Loss: frontal < other electrode sites: $Ps < 0.05$; Gain: frontal vs. temporal: $P = 0.12$). The interaction of Caudality × Hemisphere was marginally significant ($F(4,76) = 2.73$, $\varepsilon = 0.59$, $P < 0.07$).

Table 4 – Mean SPN amplitude (μV) for each preceding outcome condition, indicating an interaction of Caudality × Preceding outcome

	Gain 50	Gain 10	Loss 10	Loss 50
Frontal [**]	−1.86 (0.80)	−0.71 (0.76)	−0.26 (0.70)	0.03 (0.78)
Central [*]	−3.98 (0.79)	−2.99 (0.81)	−2.37 (0.71)	−2.64 (0.85)
Parietal	−3.92 (0.64)	−2.90 (0.73)	−2.55 (0.61)	−2.78 (0.70)
Occipital	−2.99 (0.57)	−2.45 (0.76)	−2.54 (0.66)	−2.51 (0.59)
Temporal [a]	−2.24 (0.51)	−1.64 (0.53)	−1.61 (0.59)	−1.50 (0.49)

Standard errors of the mean are in parentheses.
Note. The SPN was larger following Gain 50 outcomes than following other outcomes.
[a] $P < 0.10$.
[*] $P < 0.05$.
[**] $P < 0.01$.

3. Discussion

The main purpose of this study was to clarify the affective and motivational influences on the MFN and SPN by relating those components to choice behavior, reward anticipation, and reward evaluation.

3.1. *Choice behavior*

Consistent with Gehring and Willoughby (2002), we found that the worse the outcome on one trial, the riskier the choice on the subsequent trial. Thus, the probability of a risky choice was higher after a Loss 50 trial than after the other outcome conditions.

3.2. *Reward anticipation and the SPN*

A central goal of our study was to examine how previous outcomes would alter the SPN that develops during the waiting period prior to the outcome, in order to clarify the role of expectancies in the effects of prior outcome on risk-taking and the MFN. Importantly, in the present study, the amplitude of the SPN differed depending on previous outcomes. The SPN was larger after a Gain 50 trial than after other outcomes, regardless of the amount chosen on the current trial. In addition, the effect of preceding outcomes on the SPN was observed over frontocentral regions. This result seems to be consistent with previous reports (Kotani et al., 2003; Ohgami et al., 2004), which found a prominent effect of reward on the SPN over frontocentral regions. Thus, our result suggests that the motivational state represented by the SPN became much higher on the trials following a large monetary

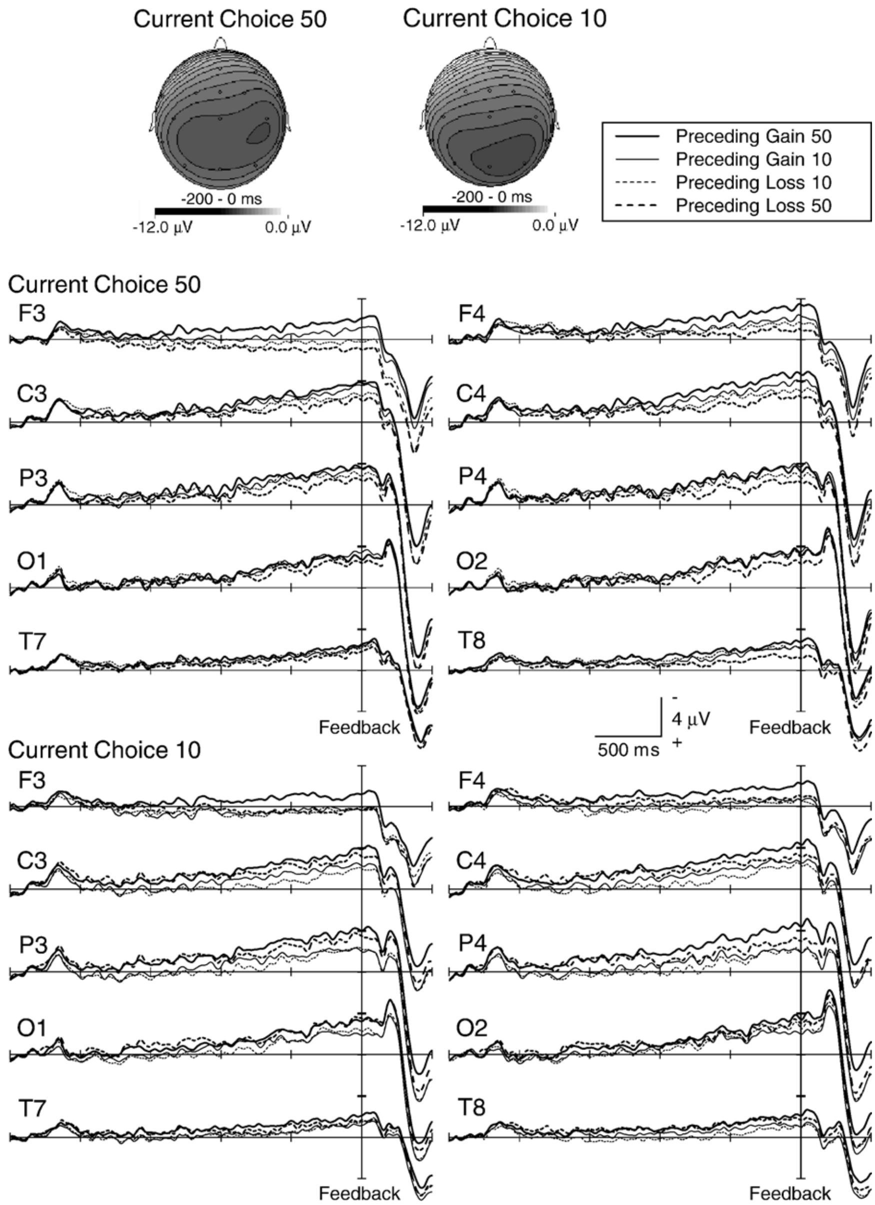

Fig. 5 – The subtracted SPN waveforms for each previous outcome case on Current choice 50 trials (top) and for each previous outcome case on Current choice 10 trials (bottom). The SPNs are depicted from the response onset, 2.5 s preceding the feedback signal. Vertical lines represent the feedback signal onset. The SPNs showed steeper slopes about 1 s before the feedback signal. Scalp distributions of the subtracted SPNs for the Gain 50 condition on both Current choice 50 and Current choice 10 are also shown above these waveforms.

gain. The trend-level interaction between current choice and previous outcome suggests that the different levels of prior outcome may influence the SPN more on Current choice 50 trials than on Current choice 10 trials, perhaps because of a lower motivational state associated with a choice of 10.

Although our results showed the SPN to be related both to performance and to motivational properties of the feedback, the pattern of results presents some challenges for interpretation. Drawing a broad distinction, one might hypothesize either that the SPN reflects anticipation of a positive (gain) event or that it represents anticipation of a negative (loss) event. If it reflects anticipation or preparation for a positive event, then the effects of sequence length on the SPN and on the probability of a risky choice would be consistent with a gambler's fallacy. Gains are seen as more likely after a run of losses, with the SPN reflecting greater anticipation or preparation for a subsequent gain. Behavior becomes riskier in such conditions to take advantage of the greater perceived likelihood of a positive outcome. A run of gains leads to the opposite pattern, with more cautious responding and anticipation of losses.

It is still plausible, however, that the SPN reflects anticipation of a negative event rather than a positive event, which would be in line with some suggestions that the SPN reflects

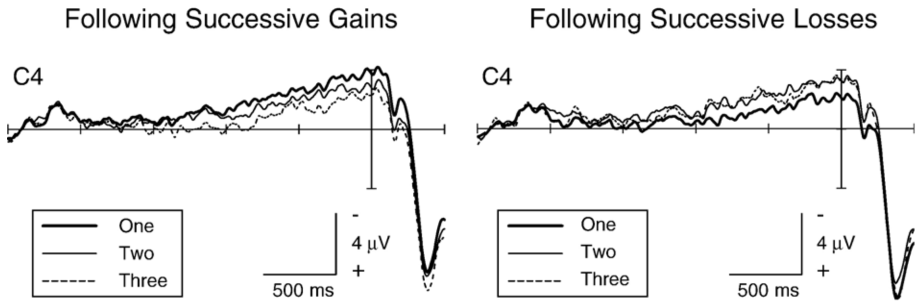

Fig. 6 – The effect of successive outcomes on the SPN delivered from C4. The SPN increased after successive Losses and decreased after successive Gains.

an anxiety/arousal state (Böcker et al., 2001; Takeuchi et al., 2005). For example, the SPN was larger following Gain 50 trials than following other outcomes. Because choices were more cautious following Gain 50 trials, one could postulate that the SPN reflected anticipation of a negative event, leading to fewer risky choices. Also consistent with a relationship of the SPN to a negative anticipatory state is the idea of a “winning streak” or a “losing streak:” losses would be seen as more likely following a run of losses, and gains more likely following a run of gains. In that case, the larger SPN following losses would reflect the greater subjective probability of loss (i.e., the anxiety/arousal state). Still, however, this interpretation is difficult to reconcile with the observation of riskier choices following losses.

In summary, although we demonstrated that the SPN was related to the motivational significance of the previous outcomes, as proposed in the Introduction, the data are ambiguous with respect to the relationship between the SPN and a particular negative or positive motivational state. It will be beneficial to future studies to incorporate richer subjective and performance measures that allow a finer-grained analysis of the subjects' motivational state during the period corresponding to the SPN. In particular, incorporating subjective measures such as confidence ratings into SPN studies may help to determine for a given context of previous outcomes whether subjects expect positive or negative outcomes.

3.3. *Reward evaluation and the MFN*

Gehring and Willoughby (2002) found that the MFN was modulated by the loss–gain valence of the outcome, rather than by the information it delivered regarding the accuracy of the response. We observed similar results. However, the analysis using the more restricted set of conditions chosen by Nieuwenhuis et al. (2004a), which controlled for outcome value, was less clear, showing a greater negativity on loss than on gain trials only when the outcomes were errors. The reason for this discrepancy is unclear, but it should be noted on gain-correct trials that there was a *greater* negativity than on gain-error trials, which is not consistent with either possible influence on the MFN (sensitivity to losses or sensitivity to errors). In addition, the negativity peaked earlier on gain-correct trials, making it more difficult to interpret the present result: it is possible that this peak is a different, N200-like component. Other studies have noted the possibility that the MFN in studies such as this might reflect a combination of an N2 and an MFN more specific to the reward properties of the feedback (Donkers et al., 2005; Donkers and van Boxtel, 2005). Furthermore, as shown in Fig. 3, the MFN effect was absent on Current choice 10 trials, suggesting that the 10-yen rewards may not be motivating enough to produce robust effects. Despite these anomalies, on the whole, the present result is consistent with other studies that have shown evidence for motivational or incentive influences on the MFN (e.g., Takasawa et al., 1990; Holroyd et al., 2003).

Recent studies have explored the relationship between feedback-related negativities, such as the MFN elicited by gambling losses, and the ERN observed in speeded response tasks. An influential theory of the ERN, the Reinforcement-Learning theory of the ERN (RL-ERN), is intended to account for both phenomena, arguing that the speeded-response ERN and the feedback-related MFN are both reflections of a dopaminergic negative feedback reinforcement-learning signal generated when response outcomes are worse than expected (Holroyd and Coles, 2002). Recently, Nieuwenhuis et al. (2004a) presented a study in support of this theory. They devised a task in which the perceptually salient color change indicated the correct/error dimension rather than the gain/loss dimension of the outcome stimuli. They showed that, in their version of the task, error feedback elicited a larger MFN than did the correct feedback, irrespective of the gain/loss status of the outcome. They suggested that their results showed that the MFN could be sensitive to either type of information, depending on which is perceptually more salient.

A different possibility is that the MFN is not sensitive to error/correct or gain/loss distinction per se. Rather, in both cases, subjects view the stimulus as global “good/bad” feedback, indicating how well they are doing according to the standards set by the experimenter (see Yeung et al., 2005 for a similar interpretation). When a perceptually salient stimulus attribute affords that information, the MFN can provide a rapid assessment of the feedback along that dimension. Future studies will be needed to evaluate this hypothesis.

Gehring and Willoughby (2002) asserted that the higher probability of a risky choice following a prior loss than following a gain was related to the difference in the motivational state induced by a prior loss and that induced by a gain. The interpretation was supported by evidence that the previous outcomes affected MFN amplitudes and risky choices similarly. According to this line of reasoning, such a change in motivational state could affect the tendency to take risks for a number of reasons: a loss might have seemed less likely after a prior loss (the gambler's fallacy) or a loss could have induced a change in the subjective value of the options (perhaps via a context effect similar to a framing effect).

However, in this study, we found that prior outcomes affected MFN and the probability of a risky choice differently: as in the Gehring and Willoughby (2002) study, riskiness increased following losses (i.e., 50 yen choices were most frequent after Loss 50 and less frequent after Gain 50). Contrary to their finding that the MFN was larger following large losses, however, the MFN in the present study was smallest following high loss trials, especially when the choice was risky. In addition, pattern of data observed for the SPN mirrored that of the MFN.[3] Across the two studies, then, this dissociation between the MFN and the probability of risky choices suggests that the underlying process of risk-taking behavior facilitated by a previous bad outcome can be independent of the affective-motivational processing that influences the MFN (and the SPN). One possible methodological reason for the discrepancy is that the waiting period prior to the outcome was longer in the current study (2.5 s) than in Gehring and Willoughby (2002) (1 s). A longer waiting period could permit different processes to engage prior to the outcome stimulus, affecting the evaluation reflected by the MFN. For example, an expectancy similar to the gambler's fallacy could drive the MFN at short cue–feedback intervals, whereas a winning streak/losing streak expectancy could drive it at longer intervals. As with the SPN, subjective measures may help to identify the factors that control the relationship between the motivational process associated with risk-taking behavior and the evaluative process reflected by the MFN.

3.4. Implications

Our study is consistent with the growing literature showing a relationship between the MFN elicited by negative feedback and evaluative processing. Taken together, we replicated the findings of Gehring and Willoughby (2002) that (1) choices were riskier following large losses than following large gains and (2) the loss–gain status influenced the MFN response whereas the error–correct status did not (cf. Nieuwenhuis et al., 2004a,b). However, the effects of previous outcomes on the MFN and risk-taking behavior contrasted with the results of Gehring and Willoughby (2002). Although the trend of greater risk-taking after a greater monetary loss seems to be a fairly robust effect, a consideration of our data and the Gehring and Willoughby (2002) report suggest that there can be dissociations between the behavioral changes associated with post-loss risk-taking and the MFN and the SPN. The dissociation suggests that a profitable research strategy will consider the functional relationships between the behavioral control system that causes responses to be riskier following a monetary loss, a second possibly related system reflected by the SPN that causes an anticipatory motivational state to be greater following a monetary gain, and finally, the evaluative system reflected by the MFN.

4. Experimental procedures

4.1. Participants

Twenty participants (13 men), aged 19–26 years (mean ± SD = 22.9 ± 2.0), were recruited from the Waseda University community and paid for their participation (500 Japanese Yen/hour: US$4.78). All participants had normal or corrected-to-normal vision, a mean handedness score of +79.6 (Oldfield, 1971) and informed consent was obtained.

4.2. Procedure

We used a monetary gambling task similar to that of Gehring and Willoughby (2002), differing from that study in the time intervening between the choice and outcome. As in that study, participants' choices were followed by feedback signifying both the monetary gain or loss resulting from their choice and the potential gain or loss had the other option been chosen.

Each trial began with the presentation of a white fixation spot between two blank squares (subtended visual angle 1.1° × 1.1°) displayed centrally on a Sharp LL-T17A1 monitor 80 cm in front of the participant (Fig. 7). After 800 ms, a "10" or a "50" (alternatives) appeared in each square. Participants were instructed to choose one square by pressing a button with their right index or middle finger (corresponding to the left or right square, respectively). The fixation disappeared upon the button press, but the squares and numeral remained. 2.5 s after the choice, the color of the numeral and square turned red or green, informing participants of the outcome. Green would indicate that the amount represented by the chosen numeral (Japanese Yen) was added to the total amount awarded to the individual at the end of a block of trials, red indicated that the amount would be deducted from the total. Simultaneously, the square not chosen also changed color to indicate to the participant what they would have gained or lost had they chosen the other square.

For example, a loss of 10, when the unchosen alternative was a loss of 50, actually corresponded to the most advantageous ("correct") choice; it was the better of the two outcomes. On the other hand, a gain of 10, when the unchosen alternative was a gain of 50, corresponded to the disadvantageous ("error") choice—the chosen response was less consistent than the alternative with the overall goal of maximizing gains and minimizing losses. In addition to these "loss-and-

[3] We also calculated correlations between the MFN (FCz) and the SPN (C4) amplitudes, which would be sensitive to individual differences. We found a mild positive correlation between these ERPs for Gain 50 on current-choice 50 ($r = 0.56$, $P < 0.05$), suggesting that the participants who showed larger MFNs also showed larger SPNs on trials following Gains of 50 yen.

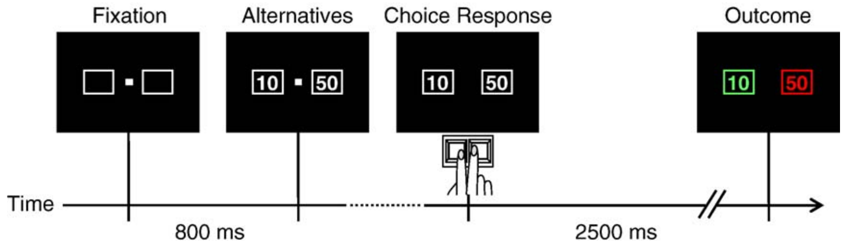

Fig. 7 – Sequence of stimulus and response events in the gambling task. In the example shown above, the "10" and surrounding box turn green, the "50" and surrounding box turn red.

correct" and "gain-and-error" conditions were "loss-and-error" and "gain-and-correct" conditions (Gehring and Willoughby, 2002).[4]

Inter-trial intervals ranged from 0.8 to 1.2 s in a randomized fashion (increments of 200 ms). Eleven of the participants were assigned green as the gain color and nine were assigned red as the gain. The experimental session consisted of 20 blocks of 32 trials each, separated by short breaks. Each participant initially received an allotment of 2000 Japanese Yen and was informed of the current total amount at the end of each block. Both losses and gains were accumulated across blocks.

Before the experimental session, the participant performed a control task (2 blocks of 64 trials), in which the identical stimuli used in the gambling task were presented with the same temporal order, but instead of the feedback signal, the squares disappeared. The participant was asked to respond by pressing the left or right button with the right index and middle finger, respectively, and then to keep gazing at the fixation until the squares disappeared. This control task was used to estimate the movement-related potentials associated with button press.

4.3. *Recording*

The electroencephalogram (EEG) was recorded from 28 electrodes (Fp1, Fpz, Fp2, F7, F3, Fz, F4, F8, FC1, FCz, FC2, FC5, FC6, T7, C3, Cz, C4, T8, CP5, CP6, P7, P3, Pz, P4, P8, O1, Oz, and O2; American Electroencephalographic Society, 1991) with tin electrodes embedded in a nylon mesh cap (Electrode-Cap International, Eaton, OH). The left ear lobe served as the reference. An averaged ear lobe reference was derived off-line using right ear lobe data. For the detection of artifacts, the vertical and horizontal electrooculogram (EOG) was recorded from left supraorbital and infraorbital electrodes and left and right outer canthus, respectively, with tin electrodes. A ground electrode was placed on the forehead. The time constant and high frequency cut-off for the EEG and EOG were 10 s and 100 Hz, respectively. Electrode impedances were below 5 kΩ. The EEG and EOG were amplified by the BrainAmp amplifier (Brain Products, Inc.). All signals were digitized on-line at a rate of 250 Hz. All trials in which EEG voltages or both vertical and horizontal EOG voltages exceeded a threshold of 100 mV during the recording epoch were excluded from further analysis. The trials containing muscular activity were also discarded. EEG data were corrected for ocular movement artifacts using the procedure described by Gratton et al. (1983). After these procedures, the number of trials per average ranged from 66 to 199 for testing the Gain/Loss vs. Correct/Error status of the MFN, from 26 to 39 for testing the effect of previous outcome on the MFN, and from 50 to 76 for testing the effect of previous outcome on the SPN.

Table 5 – Possible combinations of chosen outcome and alternative outcome

Chosen outcome	Alternative outcome	Condition
−50	−10	Loss and error
−50	+10	Loss and error
−50	+50	Loss and error
−10	−50	Loss and correct*
−10	+10	Loss and error
−10	+50	Loss and error*
+10	−50	Gain and correct*
+10	−10	Gain and correct
+10	+50	Gain and error*
+50	−50	Gain and correct
+50	−10	Gain and correct
+50	+10	Gain and correct
+50	+50	Gain
−50	−50	Loss
+10	+10	Gain
−10	−10	Loss

Note. We averaged the MFNs for 4 conditions derived from 12 combinations of chosen and unchosen amounts (Fig. 1b, left panel). Asterisks indicate the four conditions that are analogous to the four conditions chosen by Nieuwenhuis et al. (2004a); these conditions should reduce superimposition of the P300 on the MFN (Fig. 1b, right panel). We excluded from averaging the equivalent-option cases, shown in the last 4 conditions.

[4] Note that the terminology "correct" and "error" in this case has a specific meaning: an error occurs when one response would have been preferable to the response that was actually executed. Such a definition is consistent with the definition of "error detection" in the work of Coles and colleagues, where error detection occurs by comparing the response that ought to have been executed with the response that was actually executed (Bernstein et al., 1995; Scheffers and Coles, 2000). The use of these terms in the present case presumes that subjects had the goal of maximizing gains and minimizing losses.

4.4. Data analysis

4.4.1. Risky choice influenced by preceding outcomes

Gehring and Willoughby (2002) found that a risky choice (i.e., choosing 25¢ rather than 5¢) depended on the outcome on the preceding trial. Participants made riskier choices when the immediately preceding outcome was a loss than when it was a gain. We calculated the proportion of risky choices by dividing the number of 50-yen choices by the total number of trials, according to the previous outcome (i.e., Gain 50, Gain 10, Loss 10, and Loss 50). Both the SPN and the MFN were also averaged according to these categories.

4.4.2. The medial frontal negativity (MFN)

To obtain the MFN, ERPs were averaged using the feedback signal as a trigger according to previous outcomes (i.e., Gain 50, Gain 10, Loss 10, and Loss 50) and the combination of correctness and outcome (i.e., loss/error, loss/correct, gain/error, and gain/correct). In the latter case, we first averaged the MFNs based on 12 of the 16 feedback types (Table 5). However, that subset confounded the correct vs. error comparison with differences in the amount of gain vs. loss, which would affect the P300 amplitude (i.e., larger P300s are elicited by large gains and losses than by small gains and losses) (Nieuwenhuis et al., 2004a). Thus, to reduce the influence of the P300 on the MFN, we also averaged the MFNs from 4 conditions chosen by Nieuwenhuis et al. (2004a) to eliminate this confound. The averaged waveforms were digitally filtered with a 12 Hz low-pass filter (24 dB/octave roll-off). The MFN was quantified as the mean amplitude at FCz in the 200–300 ms epoch following the onset of the feedback stimulus, relative to a 100 ms pre-stimulus baseline. In the analysis of gain/loss effect based on previous outcomes, peak amplitude of the difference wave at FCz obtained by subtracting the ERP on the gain trials from the ERP on the loss trials was measured relative to a 100 ms pre-stimulus baseline (i.e., maximum amplitude within the 170–320 ms latency time window).[5]

4.4.3. The stimulus-preceding negativity (SPN)

Brunia (1988) observed a right hemisphere preponderance of the SPN, reflecting an expectancy of the following feedback stimulus. In contrast, the readiness potential has a contralateral preponderance of negativity (i.e., negative slope, Shibasaki et al., 1980), that is, a larger amplitude over the left hemisphere when the responding limb is the right hand. If the readiness potential is cancelled out by a subtraction method (Damen and Brunia, 1994), only the non-motoric stimulus preceding negativity would remain as an index of the magnitude of anticipation. Thus, to assess the SPN prior to the feedback signal, we subtracted the ERP in the control task from that in each condition.

Mean SPN amplitudes over the 200 ms interval preceding the feedback signal were calculated at F3, F4, C3, C4, P3, P4, O1, O2, T7, and T8, referenced to a baseline of 200 ms after the response (i.e., 2500–2300 ms before the feedback signal). The SPN amplitude measurement in each choice (i.e., choice of 50 vs. 10) was subjected to a three-way ANOVA with repeated measures on the variables of Previous-outcome (Gain 50/Gain 10/Loss 10/Loss 50), Hemisphere (left/right), and Caudality (frontal/central/parietal/occipital/temporal). Where multiple comparisons were required, the Newman–Keuls test was employed. The degrees of freedom were adjusted with the Greenhouse–Geisser procedure, but the original degrees of freedom are reported with the epsilon value (these corrections were also applied to performance and MFN measures).

We also averaged the SPNs according to the number of successive prior gains or losses. The SPNs after one Gain, after two successive Gains, and after three successive Gains were calculated, as were the SPNs after one Loss, after two successive Losses, and after three successive Losses. Gain trials were pooled across Gain 10 and Gain 50 trials, and Loss trials pooled across Loss 10 and Loss 50 trials. If subjects behave according to the Gambler's fallacy, they should expect a gain after a run of successive losses and a loss after a run of gains. Thus, if the SPN is more sensitive to the anticipation of positive outcomes, it should increase after successive losses; if the SPN is more sensitive to negative anticipation, it should increase after successive gains.

[5] Different analyses required different measures of MFN amplitude. Because one of our aims was to compare ERPs across gain/loss and correct/error statuses, we scored mean amplitudes referred to the baseline; the Gain-Correct trials did not elicit a distinct MFN peak to use in scoring the negativity. On the other hand, we scored the peak amplitude of the difference wave (Loss-Gain) to investigate the influence of previous outcomes on the MFN. In these analyses, the difference waves showed distinct deflections that allowed the peak amplitude to be scored. However, there were sometimes two peaks in a difference wave; in such cases, we scored the peak that was distributed more frontal-centrally.

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