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Research report

Cardiac concomitants of performance monitoring: Context dependence and individual differences

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Abstract

Feedback processing is an important aspect of cognitive control and decision-making. Several studies have shown that heart rate slows following feedback that indicates incorrect performance or loss of money. The current study was the first to investigate (1) whether this slowing reflects an evaluation of the valence of the outcome or a system that indicates that the feedback contains informative value, (2) whether the slowing is determined by the value of the outcome relative to the range of possible outcomes, and (3) whether highly anxious individuals have a hypersensitive feedback monitoring system. The results showed that heart rate only slows when the feedback is performance based. The information provided by negative feedback is processed in a context-sensitive manner, suggesting that heart rate slowing following feedback reflects a signal associated with informative value for subsequent performance adjustment. Highly anxious individuals showed larger heart rate slowing in response to feedback indicating high stakes, but they failed to respond to feedback in a context-sensitive manner. These results were interpreted to suggest that anxious individuals are generally more sensitive to performance outcomes. Heart rate changes following informative feedback proved to be a sensitive index of component processes associated with performance monitoring.

Theme: Neural basis of behavior
Topic: Cognition

Keywords: Heart rate; Performance monitoring; Gambling; Decision-making

1. Introduction

Performance monitoring is an important component of decision-making and cognitive control. This ability is specifically required when individuals make errors or when feedback indicates that performance should be adjusted [24,35]. Monitoring external signals from the environment permits the adjustment of response settings in order to prevent errors from recurring in the future. There is an increasing interest in the electrophysiological and autonomic mechanisms responsible for evaluating performance feedback and motivational significance of ongoing events [15,42,52]. These psychophysiological measures have proven especially valuable for studying the covert components of performance monitoring that cannot be accessed on the basis of performance indices only [47]. For example, these measures can inform us to what extent outcome monitoring is related to performance, and how the system identifies which outcomes are more meaningful than others.

2. Cortical and autonomic correlates of performance-monitoring

The study of error and feedback monitoring has benefited from the discovery of a frontally located negative brain potential, called the Error Related Negativity (ERN) that

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peaks approximately 50–150 ms after individuals make an error [13,16]. A similar brain potential is elicited following the delivery of negative feedback. This feedback-related negativity (feedback-ERN), or Medial Frontal Negativity (MFN), peaks approximately 250–300 ms after feedback presentation [24,35,36,52]. The feedback-ERN/MFN is elicited by feedback stimuli associated with unfavorable outcomes, such as incorrect responses and loss of money [15,24,34–36]. Source localization studies examining the underlying neuroanatomical mechanisms of the ERN/MFN have shown that the resolution of error- and feedback-related conflict is centered in or very near the anterior cingulate cortex (ACC) [3,6,34].

Although heart rate changes are commonly associated with hot emotion or stress, there is a compelling body of research demonstrating a link between sensory attention and heart rate (see reviews by Bohlin and Graham [2]; [17,27,29,38,41]; van der Molen et al. [48]). For example, Lacey [31], developed a paradigm that examined the time between sequential heartbeats as participants anticipated the occurrence of a stimulus with the instruction to react as quickly possible. Intuitively, a brief fixed foreperiod creates a focused attention and alertness that should alter heart rate if such states are related to attention to sensory input. Indeed, the time between heartbeats increased (heart rate slowed) as the time of stimulus occurrence approached. A series of recent studies suggested that the slowing of the heartbeat is due to a centrally-initiated inhibitory process (for reviews, see Ref. [28]).

Using a Wisconsin Card Sorting Task (WCST), Somsen et al. [42] showed that heart rate slowed in anticipation of both a card presentation and also following feedback. The WCST shifts category rules without warning, and therefore participants receive unexpected negative feedback after a card has been misclassified according to the new rule. In Somsen et al.'s study, heart rate slowing following feedback was magnified whenever feedback was negative, indicating that the participant's current concept was no longer valid. This finding was interpreted to suggest that the negative feedback triggered inhibition of ongoing processing. Similar work using a go–nogo paradigm and the conjoint measurement of error-related cortical negativity and heart rate slowing yielded the typical pattern of error-related negativity and subsequent error-related positivity when subjects failed to successfully inhibit their motor responses. Heart rate slowed following these errors as well, and its timing suggested a relationship with the error-related positivity; a brain potential following the ERN associated with awareness of errors [45]. In summary, heartbeat timing seems to slow down whenever task monitoring detects an error requiring a reconceptualization of the task.

3. The present study

An important question with respect to feedback-related cardiac changes is whether cardiac slowing depends on (1) whether the feedback is positive or negative (valence of the feedback), and/or (2) whether the feedback can be used to adjust subsequent actions (informative value of the feedback). Using a variant of the Iowa Gambling Task [1], we previously examined whether heart rate is sensitive to the magnitude of loss [11]. Individuals were asked to choose cards from decks that could result in a fixed gain or in varying amounts of loss. The loss was given unexpectedly, and the decks differed in the frequency with which punishment was given. We showed that heart rate slowing was more pronounced when the magnitude of loss was larger, but also when the negative feedback was given infrequently and was therefore unexpected. These results suggest that heart rate slowing following negative feedback is associated with the extent to which the feedback holds informative value for performance adjustment (see also Ref. [42]).

Van der Veen et al. [49], however, studied the cardiac changes associated with performance-related and performance-unrelated feedback and reported that heart rate slowing was associated with the valence of negative feedback rather than the performance-related information that is provided by it.

In contrast, we found in a different series of studies that heart rate slowing is related to informative negative feedback and is typically associated with the extent to which feedback needs to be evaluated [10,12]. In these studies, participants were asked to sort stimuli, and this action was followed by positive or negative feedback (following Ref. [24]). Heart rate slowed in response to performance-related negative feedback, but not in response to negative feedback that was unrelated to performance outcome. Most importantly, heart rate also slowed following unexpected positive feedback. These results suggest that heart rate is sensitive to monitoring feedback outcome for the purpose of adjusting future performance (see also Ref. [28,46]).

One goal of the present study was to address the valence versus informative issue by designing an experiment in which participants could not control the outcome of their choices. In Experiment 1, participants were asked to gamble on stimuli that could be associated with winning or losing money by pressing the space bar. A crucial feature of this design was that the feedback was not related to a performance choice (see also Ref. [52]). This design allowed us to examine whether cardiac slowing following negative feedback is related to valence per se, or whether cardiac slowing only occurs when feedback is actually related to performance.

The second goal of this study was to study the role of the context in which positive and negative feedback are given. Several ERN studies have shown that the feedback-ERN is sensitive to context. Gehring and Willoughby [15] recently studied how ACC, reflected in an ERN-like brain potential, responds to outcomes that inform future decisions in a gambling task. Participants were asked to make 2-choice gambling decisions. Their choices were followed by outcome events signifying either the monetary gain or loss that resulted from their choice, and the gain or loss that would have resulted from making the other choice. A medial frontal negative (MFN) potential was reported following loss, similar to the feedback-ERN. However, the sensitivity to losses was not simply a reflection of detecting an inappropriate choice; gains did not elicit the medial–frontal activity when the alternative choice would have yielded a greater gain, and losses elicited the activity even when the alternative choice would have yielded a greater loss. In a separate experiment, Nieuwenhuis et al. [36] replicated this effect and demonstrated that the feedback-ERN/MFN can be sensitive to both gain/loss and error/correct information conveyed by the feedback, depending on which aspect of the stimulus is made most salient. Thus, these results indicate that the system that produces the ERN (purportedly ACC) bases its evaluation on different types of information, and therefore operates in a context-sensitive manner. In a similar vein, Holroyd et al. [26] recently showed that the feedback-ERN is smaller for the same amount of loss, when this loss is presented in the context of losing even more. They concluded that the system that produces the feedback-ERN determines whether an event is good or bad in a context-sensitive manner.

To examine whether heart rate changes would demonstrate similar context-sensitivity, we compared heart rate slowing to positive and negative feedback within different contexts of gain and loss in Experiment 2. In prior studies, we found that heart rate slowing is larger when feedback is unexpected [42] or has informative value [10,12]. If heart rate slowing reflects a system that computes whether feedback is worse than expected (i.e., informative value sensitivity), then heart rate slowing should be larger for the same amount of loss when this loss is presented in the context of the possibility of losing even more. If heart rate slowing reflects a system that is sensitive to the detection of an error or a negative event (i.e., valence sensitivity), then it should be similarly sensitive to feedback indicating a certain amount loss (i.e., sensitivity to the absolute value or valence), independent of the context in which this loss is presented.

The third goal of the study was to examine individual differences in the cardiac response to performance feedback. Previous studies examining individual differences in performance monitoring have reported that anxious individuals, who worry excessively or exhibit obsessive–compulsive symptoms, have a hypersensitive performance monitoring system (see also Refs. [14,18–20,29]. Hajcak et al. compared the response-related ERN of high and low anxious participants following errors when they were performing a modified Stroop task. This study indicated that high anxiety individuals have an enhanced response-ERN magnitude following errors [14,19]. High anxiety individuals also show a greater skin conductance rise following errors, suggesting that hypersensitive performance monitoring can be extended to the autonomic domain [21]. These findings are consistent with behavioral studies showing that anxious individuals are typically hypervigilant, indicating that they selectively attend to threatening information and interpret ambiguous events in a relatively threatening way. Therefore, they are more prone to detecting imagined danger and are resistant to corrective information about these threats (for reviews, see Refs. [23,32,44].

A different interpretation is that anxious individuals are defensive when they cope with negative outcomes. Support for this hypothesis comes from studies showing that high anxiety individuals exhibit anticipatory defense towards possible negative outcomes, which leads to reduced monitoring of actual negative performance results [44]. This interpretation does not mesh with Hajcak et al. [19,20], who suggested that anxious individuals have a hypersensitive monitoring system for external cues indicating negative events and therefore should be more responsive to external cues indicating that performance outcomes are worse than expected [19,20].

The current study sought to examine the defensive versus hypersensitive hypotheses by examining cardiac changes following gain and loss in individuals with high and low anxiety levels. The analyses focused on two aspects of performance monitoring: feedback anticipation and feedback processing. Following the defensive hypothesis, anxious individuals should show larger cardiac slowing in anticipation of feedback that could indicate high loss. Following the hypersensitive hypothesis, anxious individuals should be primarily sensitive to the actual feedback.

4. Experiment 1

The first experiment addressed the issue of whether heart rate slowing that occurs following loss is associated with valence of feedback or with informative value of feedback after the participant makes a performance choice. Subjects performed a gambling task in which they were asked to press the space-bar on a keyboard in response to numbers indicating the amount of money that could be won or lost. After indicating their response, the actual feedback was displayed on the screen. The experimental task consisted of four conditions, with three possible outcomes for each condition. Because participants were only asked to press the space bar, and therefore there was no possibility for a performance choice, outcome was not related to performance. In addition, outcome valence and magnitude were related to the magnitude and color of the number. The reason for including the magnitude and color manipulations within the current design was to create similar complexity with Experiment 2, and thereby allowing comparison of the current results with findings of Experiment 2. However, in Experiment 1, we were only interested in effects of valence.

If heart rate changes following negative feedback are associated with valence (Van der Veen et al., 2004), then heart rate slowing should be more pronounced following loss than following gain. However, if heart rate slowing following negative feedback is specifically related to performance-related feedback [10,19], then there should be no difference between heart rate slowing following loss and heart rate slowing following gain.

5. Methods

5.1. Participants

Seventeen undergraduate students participated in Experiment 1 and took part in the experiment for course credit. All participants were between 18 and 40 years of age. Participants received course credits for their participation, plus a performance-related bonus. All participants were healthy according to self-report and had normal or corrected-to-normal vision.

5.2. Stimuli

Stimuli were presented on a black background with a 17-in. computer screen placed at a distance of 150 cm from the participant. Each experimental block involved a set of four different stimuli. Stimuli were numbers 4 or 8 (approximately 10 cm wide and 10 cm high) presented in red or green. Feedback signals consisted of a positive or negative number of the same size presented in white, indicating that the participant was rewarded or penalized on that trial, or that there was no gain or loss (zero).

5.3. Experimental task

Participants sat comfortably about 1.5 m in front of a computer screen in a quiet dimly lit room. On each trial, participants saw a stimulus consisting of the numbers 4 or 8 in green or red. Participants were asked to press the space bar in response to the stimulus. Stimulus presentation was response-terminated. The response initiated a black screen for 1500 ms that was terminated by the 1500 ms feedback stimulus. A new stimulus was presented following a variable interval of 1000–2000 ms. The interval between consecutive stimuli was approximately 5.5 s (see Fig. 1A). Participants performed eight blocks of 64 trials. In each block, each stimulus was presented 16 times in a pseudo-random order, resulting in 128 trials for each condition. The left panel of Fig. 1B presents the gain and loss scheme for each stimulus.

The four stimuli could each result in a win, loss, or no change in points. The green 4 resulted in a 1-point loss (25%), a 0-point loss (50%), or a 1-point gain (25%). The red 4 resulted in a 2-point loss (25%), a 0-point loss (50%), or a 2-point gain (25%). The green 8 resulted in a 2-point loss (25%), a 0-point loss (50%), or a 2-point gain (25%). The red 8 resulted in a 4-point loss (25%), a 0-point loss (50%), or a 4-point gain (25%). The stimuli were presented in mixed blocks.

Before the experimental phase, participants received written instructions and performed a practice block of 64 trials. Participants began the task with a bonus of 10 euros. At the end of each block, participants were provided with information indicating the total amount of money they had

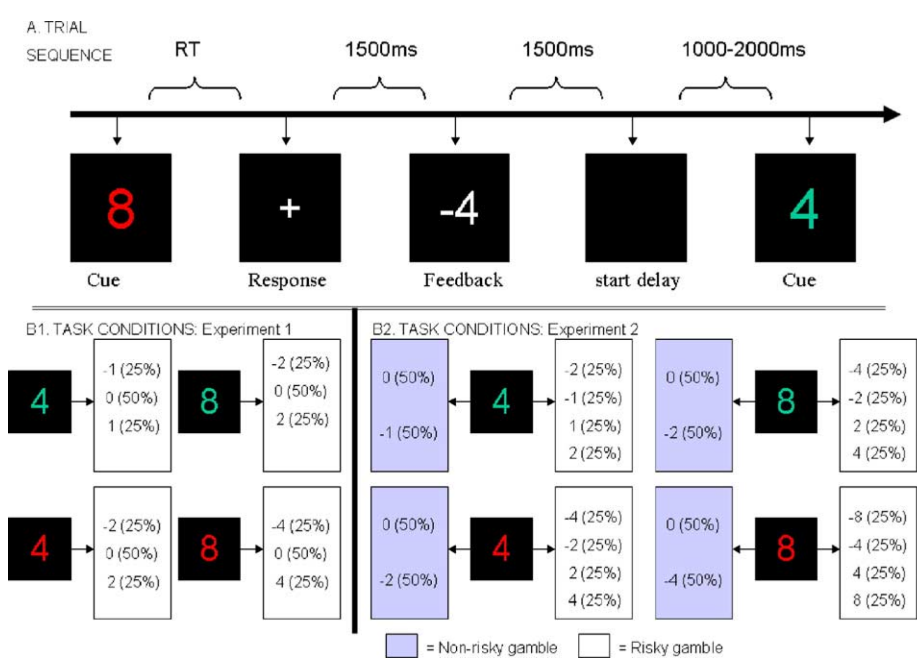

Fig. 1. A: Trial Sequence for Experiment 1 and Experiment 2. B1: task conditions for Experiment 1. The white boxes show the possible outcomes and their probabilities for each target. B2: task conditions for Experiment 2. The white boxes show the possible outcomes and probabilities for risky gambles, and the gray boxes show the possible outcomes and probabilities for non-risky gambles.

at that time. Upon completion of the experiment, participants received bonus money, which was an amount of approximately 10 euros.

To keep the participants engaged in the task, they were told that at the end of the experiment they would be asked a question about the task, but they were not informed about the nature of the question. Participants were told that if they would give the correct answer, their bonus money would be doubled. At the end of the experiment, subjects were asked to list the contingencies of one of the conditions, randomly chosen by the experimenter. All participants, except for one, were able to repeat the contingencies. Excluding this subject from the analysis did not change the results.

5.4. Recording and data analysis

During the task, electrocardiogram (ECG) and respiration were continuously recorded. The ECG was recorded from three AgAg/CL electrodes, attached via the modified lead-2 placement. Respiration was recorded through a temperature sensor placed under the nose. The signals were amplified by a Nihon Kohden polygraph and sampled by a Keithley AD-converter at a rate of 400 Hz. The recorded Inter Beat Intervals (IBIs) were screened for physiologically impossible readings and artifacts. These were corrected by estimating R-waves in the program that extracted the IBIs from the digitized ECGs. The respiration signal was used only to eliminate heart rate changes associated with sudden respiratory changes. Both inhalation and exhalation trials were included in the analysis.

The focus of Experiment 1 was on heart rate responses to the feedback in order to decide between the valence versus information interpretation. In order to assess these effects, four IBIs were selected around the feedback (IBI −1, 0, 1 and 2). These IBIs were referenced to IBI −2. An initial analysis of IBI −2 did not result in any baseline differences between the four conditions. IBI −1 should reflect effects of feedback anticipation, and IBI 0, 1, and 2 have previously shown most robust feedback related effects [10].

The 4 IBIs were submitted to an ANOVA with Color and Number factors. The Color condition reflects the differences in responses associated with the green-4 condition and the green-8 condition (on average green targets were associated with relatively lower gain and loss) versus the red-4 and red-8 condition (on average red targets were associated with relatively higher gain and loss). Likewise, the Number condition reflects the differences in responses associated with the green-4 and red-4 condition (on average low numbers were associated with relatively lower gain and loss) and the green-8 and red-8 condition (on average high numbers were associated with relatively higher gain and loss). An additional factor was Valence, which could consist of a gain, zero points, or a loss.

6. Results and discussion

6.1. Heart rate changes associated with feedback processing

An IBI × Valence and an IBI × Valence × Condition ANOVA did not result in any significant effects of Valence or Condition (all P's > 0.2, see Fig. 2), consistent with the notion that context and valence effects depend on getting performance-based feedback. It is unlikely that this effect is due to lack of power because the number of trials was larger than what we have used in previous studies in which we did find robust feedback effects [11,12,42].

The conclusions derived from these findings are twofold: (1) heart rate does not respond to valence per se, and (2)

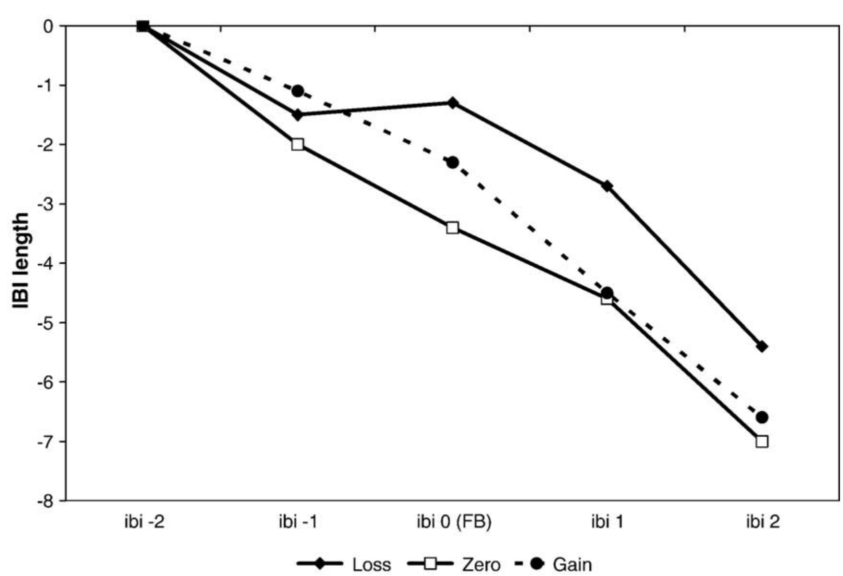

Fig. 2. Heart rate response to loss, zero points, and gain in Experiment 1. In the no-choice condition, heart rate did not respond differently to positive and negative feedback.

heart rate does not respond to feedback that has no behavioral relevance. In Van der Veen et al.'s (2004) study, the information in the (yoked) control study also had no behavioral relevance. However, in this condition and the random feedback condition in the [10,12] studies, subjects may have processed the feedback in an attempt to improve their performance.

Thus, following the informative-value hypothesis of heart rate slowing, there should be differential heart rate slowing following positive and negative feedback when participants can choose between options, rather than simply receiving feedback. This was one of the hypotheses tested in Experiment 2.

7. Experiment 2

The second experiment addressed the issue of whether heart rate slowing occurs when participants have a performance choice, and whether heart rate slowing is sensitive to context. Because the current experiment addressed different questions, the design consisted of several additional conditions with respect to Experiment 1. First, adding the possibility for participants to choose their response serves the purpose of making feedback have informative value for subsequent performance adjustment. Participants were asked to respond to the same targets as in Experiment 1, but in the current experiment, there was a possibility to alternatively make a low-risk gamble, which would result in zero points or a small loss. Thus, the participants now had the possibility to control the outcome to some extent. It should be noted that the terms low-risk and high-risk refer to the immediate outcome possibilities of each of these choices, and not to the eventual outcome in case this option would be chosen across the experiment.

A second purpose of Experiment 2 was to examine under what conditions the system that evaluates feedback resulting in heart rate slowing is sensitive to the context in which the feedback is presented. This question is important for understanding how the system actually decides which outcome is informative. A critical evaluation is the comparison between magnitude of gain and loss, and whether the absolute value is the best/worst possible outcome or not. This issue was addressed by the Number and Color coding. Each number could result in a small gain, high gain, small loss or high loss. The contingencies were chosen in such a way that the high loss in the green conditions had the same absolute value as the small loss for red conditions (see Fig. 1). Therefore, a comparison of high loss for green numbers and small loss for red numbers should indicate whether heart rate changes are sensitive to context (i.e., the context is different but the absolute value is the same). In contrast, a comparison between number 4 conditions (loss of 2) and number 8 conditions (loss of 4) reflects the effect of outcome magnitude. Thus, this selection of trials allowed us to perform a magnitude (2 versus 4) and context (worse versus worst) comparison. A similar selection of gain trials allowed us to examine the effects of context (better/best) and magnitude (2 versus 4) for winning money.

A final purpose of Experiment 2 was to study whether these cardiac changes were different for individuals with high and low anxiety levels. For this purpose, we examined heart rate changes associated with both risk anticipation and feedback processing.

8. Methods

8.1. Participants

Undergraduate students in an introductory psychology class (n = 519) completed the Dutch version of the Penn State Worry Questionnaire (PSWQ; [33]). The PSWQ is a sixteen-item self-report measure that assesses dysfunctional attitudes about worry on a five-point Likert scale (minimum score = 16, maximum score = 80). The Dutch PSWQ has excellent psychometric properties in both clinical and non-clinical populations [50]. Subjects were rank-ordered on the basis of their scores on the PSWQ. Thirty-nine subjects (7 male, 32 female) from the top of the PSWQ distribution (M = 68.9, SD = 3.9) and 42 (25 male, 17 female) who scored at the bottom of the distribution (M = 25.1, SD = 2.9) were invited to participate in the experiment. From these groups, 16 High-PSWQ (14 female, 2 male, M PSWQ = 68.4, SD = 0.8) subjects and 15 Low-PSWQ (7 female, 8 male, M PSWQ = 23.6, SD = 0.8) agreed to participate. Although no formal clinical assessment was completed, participants' scores were in the range observed in patients with Generalized Anxiety Disorder (M = 68.1, [4]).

All participants were between 18 and 40 years of age (M = 23.9, SD = 7.5), and there was no age difference between groups, $F(1,30) = 2.29$, $P = 0.14$. Participants received course credits for their participation, plus a performance-related bonus. Participants began the task with a bonus of 10 euros. At the end of each block, participants were provided with information indicating the total amount of money they kept throughout the task. Participants were paid bonus money upon completion of the experiment which could be an amount between 5 and 10 euros. None of the subjects had participated in Experiment 1.

8.2. Experimental procedure

The stimuli were similar to those of Experiment 1, and the same heart rate recording procedure was used. The experimental design was similar to that of Experiment 1. The only difference was that the four stimuli could result in different outcomes and that the participants had the possibility of making a choice between low-risk and high-risk gambles. The four stimuli could result in different outcomes based on whether participants decided to gamble or not. The gambling contingencies were explained to the participants at the beginning of the experiment (see Fig. 1B). The green-4 resulted in a 2-point loss (25%), a 1-point loss (25%), a 1-point gain or a 2-point gain (25%) in case of a high-risk gamble, and in a 0-points (50%) or a 1-point loss (50%) in case of a low-risk gamble. The red-4 resulted in a 4-point loss (25%), a 2-point loss (25%), a 2-point gain or a 4-point gain (25%) in case of a high-risk gamble, and in a 0-point (50%) or a 2-point loss (50%) in case of a low-risk gamble. The green-8 resulted in a 4-point loss (25%), a 2-point loss (25%), a 2-point gain or a 4-point gain (25%) in case of a high-risk gamble, and in a 0-point (50%) or a 2-point loss (50%) in case of a low-risk gamble. The red-8 resulted in an 8-point loss (25%), a 4-point loss (25%), a 4-point gain (25%) or an 8-point gain (25%) in case of a high-risk gamble, and in a 0-point (50%) or a 4-point loss (50%) in case of a low-risk gamble.

9. Results and discussion

9.1. Performance results

To examine whether there were differences in gambling decisions between the Anxiety-groups and conditions, a Number (4/8) × Color (Green/Red) × Group (High/Low Anxiety) ANOVA was performed for the % of trials on which the subjects made a high-risk decision. Percentages of high-risk gambles were computed as the proportion of trials on which participants decided to make a high-risk gamble of a particular condition. These values are presented in Table 1. The analysis only resulted in a main effect of Number, $F(1,29) = 6.41$, $P < 0.05$, showing that subjects more often made high-risk decisions for green-8 and red-8 trials (79.6%) than for green-4 and red-4 trials (75.0%). There was no difference between groups in percentage of high-risk decisions in general, $F(1,29) = 0.06$, $P = 0.81$, and there were no interactions between Group and any of the conditions (all P's > 0.15).

Table 1
Performance indices (means and standard errors) for low and high anxiety subjects in Experiment 2

	Green-4	Red-4	Green 8	Red 8
Low anxiety % gamble	77.9 (4.5)	81.8 (4.2)	76.0 (4.4)	78.7 (4.0)
High anxiety % gamble	70.8 (4.8)	81.2 (3.9)	75.4 (4.7)	76.6 (3.8)
Low anxiety mean RT (SD)	572 (52)	588 (60)	605 (51)	600 (58)
High anxiety mean RT (SD)	622 (65)	605 (61)	632 (63)	615 (59)

% Gamble refers to the proportion of trials on which participants made a high-gamble decision and RTs refer to high-gamble decisions only.

Although there were no speed instructions, similar analysis for RTs for only the high-risk gambling trials resulted in a main effect of Color, $F(1,29) = 5.35$, $P < 0.05$, showing that subject made faster high-risk gambles in green 4 and green 8 conditions (M = 592, SD = 38) than in red-4 and red-8 conditions (M = 619, SD = 43). Again, there was no main effect of Group, $F(1,29) = 0.84$, $P = 0.84$, or other effects for RT (all P's > 0.30).

To summarize, targets that could result in high gain or loss (green-8 and red-8) resulted in more high-risk gambles than targets that could result in small gain or loss (green-4 and red-4). Importantly, performance results were similar for high and low anxious subjects. As can be seen in Table 1, the percentage of high-risk gambling decisions was above 70% for all conditions, making the number of trials sufficient to focus our analyses on high-risk gambling trials only. The heart rate results for low-risk gambling decisions were not analyzed because of the small number of trials.

10. Experiment 2: anticipatory and feedback-related heart rate changes

A preliminary analysis on IBIs across the task of Experiment 2 did not results in a significant difference between groups in mean IBI, $F(1,29) = 0.01$, $P = 0.94$ (Low Anxiety Group, Mean IBI = 804, SD = 78, High Anxiety Group, Mean IBI = 807, SD = 192), or in Standard Deviation of IBI, $F(1,29) = 0.41$, $P = 0.53$ (Low Anxiety Group, Mean SD = 22, High Anxiety Group, Mean SD = 24).

Where interactions with IBI are reported, the main effects were also significant, except where noted.

10.1. Anticipation

Fig. 3 presents four IBIs around the response for each of the groups and four conditions. IBI −2 was the reference point. A preliminary analysis showed that there were no differences between groups and conditions in this baseline value. As can be seen in Fig. 3, heart rate slowed in anticipation of the response (IBI 0) and was followed by an acceleratory recovery (IBI 1). To examine whether this response was different between groups and conditions, three IBIs were submitted to the IBI (−1, 0, 1) × Number (4/8) × Color (Green/Red) × Group (High/Low Anxiety) ANOVA. The analysis resulted in an IBI × Number interaction, $F(2,56) = 4.06$, $P < 0.05$. This interaction shows that heart rate was slower in anticipation of feedback associated with targets that could result in high loss or gain (green-8 and red-8) than for targets that could result in small loss or gain (green 4 and red 4) at IBI 1 (Difference score = 3.89, $F(1,28) = 5.45$, $P < 0.01$), whereas this difference was not significant at IBI −1 (Difference score = 1.20, $F(1,28) = 2.86$, $P = 0.11$) or IBI 0 (Difference score = 2.0, $F(1,28) = 3.10$, $P = 0.10$). There

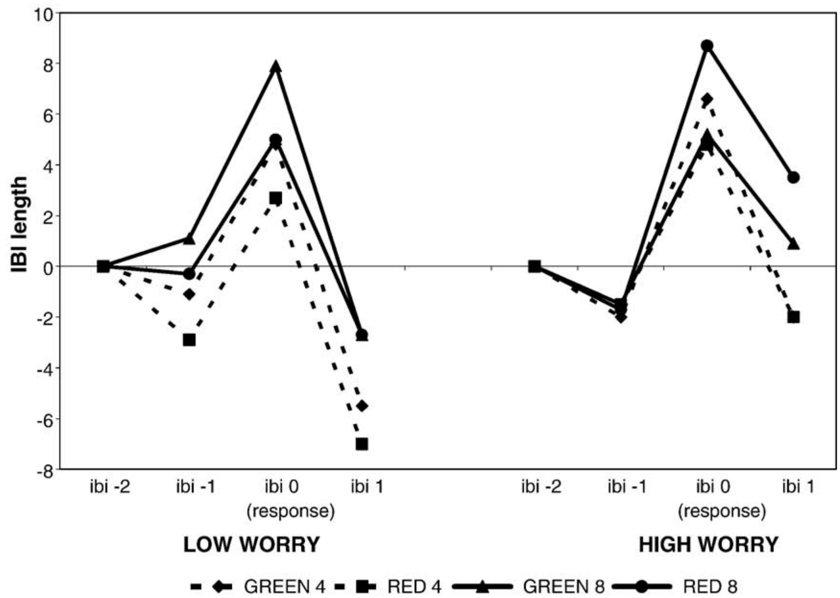

Fig. 3. High and low anxiety subjects' cardiac responses in anticipation of feedback from the green-4, red-4, green-8 or red-8 conditions in Experiment 2.

were no further main effects or interactions, and importantly, none of these effects were modulated by Group, all P's > 0.3.

Thus, heart rate slowed in anticipation of a response and was followed by an acceleratory recovery. This acceleratory recovery was less pronounced when participants anticipated feedback that could indicate high stakes compared to feedback that could indicate low stakes. Thus, conditions that were preferred most in terms of actual decisions (high stake choices) were also accompanied by increased anticipatory heart rate slowing. This effect was similar for high and low anxious individuals.

10.2. Feedback

Fig. 4 presents five IBIs around the feedback stimulus. Again, IBI −2 was the reference point and a preliminary analysis showed that there were no differences between groups and conditions in this baseline value. To examine whether high and low anxious individuals process feedback differently, four IBIs (IBI −1, 0, 1 and 2) were submitted to the ANOVA. The first 2 IBIs (IBI 1 and 2) following IBI 0 have been found to be most sensitive to the direct effects of feedback presentation [10]. The response analysis showed that the value of IBI −1 did not differ between conditions,

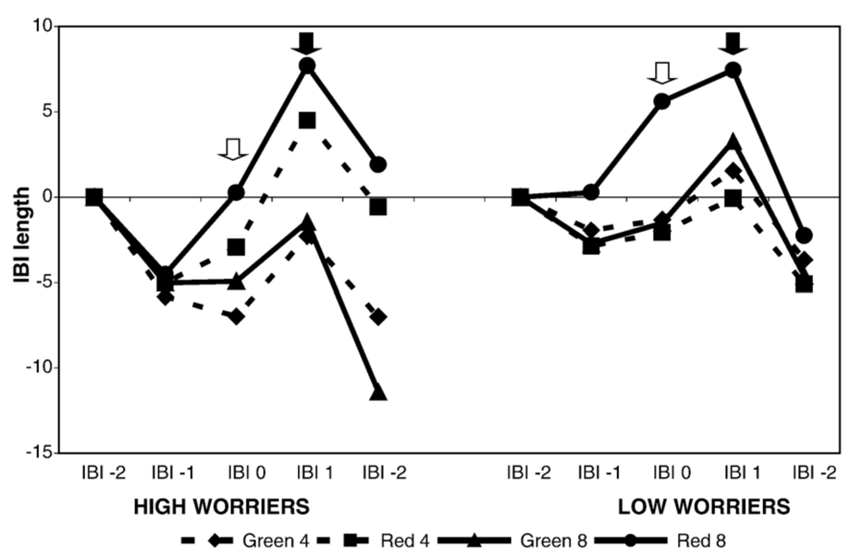

Fig. 4. High and low anxiety subjects' cardiac changes following feedback for the green-4, red-4, green-8 and red-8 conditions in Experiment 2. These values are averaged across actual performance outcomes (gain or loss). The white arrows indicate the main effect of number and the black arrows indicate the interaction with Anxiety group.

thus, the effects reported below are related to feedback processing rather than feedback anticipation.

The IBI (−1, 0, 1, 2) × Number (4/8) × Color (Green/Red) × Valence (high gain, small gain, small loss, high loss) × Group (High/Low Anxiety) ANOVA resulted in 3 important sets of interactions. First, there were interactions between IBI and Color, $F(3,84) = 6.04$, $P < 0.001$ and Group, IBI and Color, $F(3,84) = 8.55$, $P < 0.001$. Fig. 4 shows that heart rate slowing was larger following feedback in the red-4 and red-8 condition (red numbers) than for feedback in the green-4 and green-8 condition (green numbers) at IBI 0, $F(1,28) = 11.53$, $P < 0.001$, and IBI 1, $F(91,28) = 9.82$, $P < 0.001$. This difference was larger for high anxiety than for low anxiety individuals at IBI 1, $F(1,28) = 5.50$, $P < 0.05$ (Color × Group interaction). Two separate ANOVAs for each group revealed that the IBI × Color interaction was only significant for high anxiety subjects, $F(3,39) = 13.35$, $P < 0.001$, but not for low anxiety subjects, $F(3,45) = 1.67$, $P = 0.33$. Thus, this effect shows that, as expected, high anxiety individuals show a more pronounced heart rate response to feedback indicating high stakes.

The second important interaction was observed between IBI and Number (see Fig. 4). This interaction shows that heart rate slowing was more pronounced following feedback of green-8 and red-8 conditions than following feedback of green-4 and red-4 conditions. Post hoc comparisons show that this effects was only significant for IBI 0, $F(1,28) = 5.56$, $P < 0.05$, and this effect was similar for both anxiety groups (IBI × Number × Group, $P = 0.87$). Thus, this effect shows that all participants showed larger heart rare slowing for high stakes feedback (associated with high number conditions) than for low stakes feedback (associated with low number conditions). It should be noted that the IBI 0 effect could also be due to anticipation of the feedback rather than its processing. However, no such difference was observed for IBI −1 (in which anticipation effects are greatest), and in previous studies, we have also observed feedback-related differences at IBI 0 [10]. Thus, it is most likely that these effects are related to processing feedback rather than anticipating feedback.

Finally, the last interaction of importance was between IBI and Valence, $F(9,252) = 4.22$, $P < 0.001$ (see Fig. 5). This effect shows that slowing from IBI 0 to IBI 1 was larger for high loss compared to small gain, $F(3,84) = 7.98$, $P < 0.001$, but the IBI × Valence interaction for conditions did not differ form each other. Although the IBI × Valence × Group interaction was not significant, $F(9,252) = 1.33$, $P = 0.22$, post hoc comparisons for each group separately shows feedback differentiation only for low anxiety subjects, IBI × Valence, $F(9,117) = 3.21$, $P < 0.001$, as indicated by more heart rate slowing following high loss, low loss and high gain, relative to low loss. High anxiety subjects, in contrast, showed heart rate slowing to all feedback, IBI × Valence, $F(9,135) = 2.05$, $P = 0.09$. This pattern of findings is consistent with the hypothesis that high anxiety individuals are more sensitive to performance feedback, whereas low anxiety individuals only show heart rate slowing to feedback that has informative value.

Thus, the results show that the anticipatory recovery following a response choice was delayed when feedback was presented that indicated high gain or loss (i.e., high stakes) compared to feedback indicating low gain or loss (i.e., low stakes), which was true for both the Number and Color comparisons. Further, following actual outcome, heart rate slowing was larger following high loss, low loss and high gain, relative to low loss, but only for low anxiety individuals. Highly anxiety subjects showed larger heart rate slowing in response to high stakes feedback than low anxiety individuals, but did not differentiate between loss and gain.

10.3. Context effects

In Experiment 1, where there was no possibility to make a performance choice, context did not have an effect on cardiac changes. A main focus of the study was to examine how cardiac changes were sensitive to context when subjects received performance-based feedback. This set of comparisons focused on the question whether the system that initiates heart rate slowing responds to the absolute value of gain or loss, or if losing a specific amount is different in the context of the possibility of losing even more. We selected the data of interest in the following way. First, we compared losing an amount when this was the worst possible outcome (−2 for green-4, and −4 for green-8, see Fig. 1) with losing the same amount when there was a possibility of losing even more (−2 for red-4, and −4 for red-8, see Fig. 1). Thus, the actual magnitudes were the same, but the context was different. Second, we compared two magnitudes of loss; high loss (−4) versus low loss (−2). If heart rate changes result from a system that is sensitive to the absolute level of losing, then there should only be an effect of Magnitude. If heart rate is also sensitive to the context of losing, then there should be an interaction with Context. Fig. 6 presents five IBIs around the feedback for the negative and positive feedback trials.

The Context (worst, worse) × Loss Magnitude (high versus low) × IBI (−1, 0, 1, 2) × Group (High/Low Anxiety) ANOVA resulted in a Group × IBI × Context interaction, $F(3,84) = 5.12$, $P < 0.001$. As can be seen in the Fig. 5, heart rate slowing was larger after losing points when there was a possibility of losing more, compared to when the loss was the worst possible result for the low anxiety group, $F(3,39) = 5.07$, $P < 0.05$, but there was no context difference for the high anxiety group, $F(3,45) = 0.97$, $P = 0.42$.

A similar analysis for gain focused on winning a large amount when this was the best possible outcome (+2 for green-4, and +4 for green-8, see Fig. 1) with winning the same amount when it was possible to win even more (+2 for

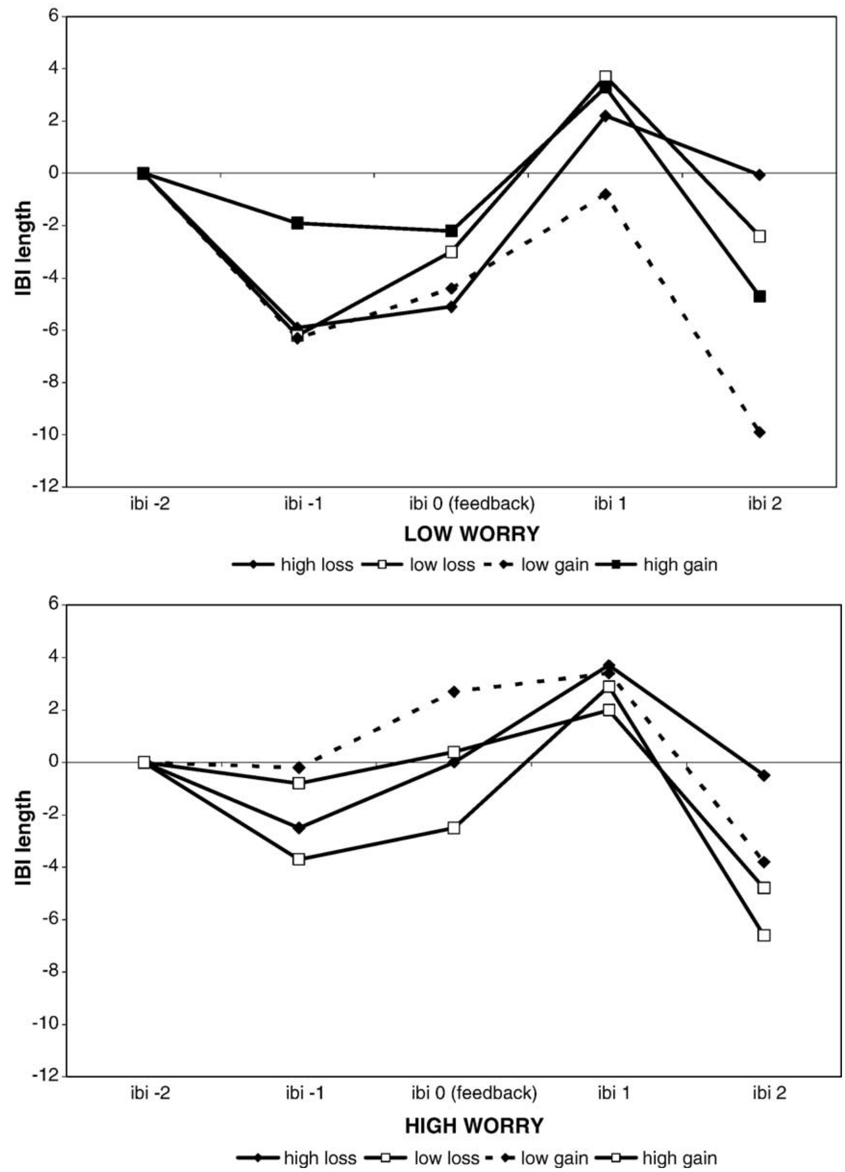

Fig. 5. Cardiac changes associated with winning and losing small and large amounts in Experiment 2, averaged across conditions, for high and low anxiety subjects.

red-4, and +4 for red-8, see Fig. 1). This analysis resulted in an almost significant interaction between IBI and Gain, $F(3,84) = 2.28$, $P = 0.09$. The effect of Gain Magnitude shows that heart rate slowing is larger for winning four points compared to winning two points. Anxiety Group or Context did not alter this effect.

To summarize, cardiac slowing following feedback seems sensitive to the context in which the feedback is delivered, and is more pronounced for the same magnitude when there is a possibility of losing more, than for the same magnitude when this is the largest possible loss. This context effect is only seen for low anxiety subjects, whereas high anxiety subjects show heart rate slowing to all negative feedback, independent of context. Finally, heart rate slowing is larger for high gain than for small gain, but this effect did not differ between high and low anxiety subjects.

11. General discussion

This study has five main findings. First, heart rate slowing following feedback occurs only when feedback is performance-related. Second, cardiac slowing associated with performance feedback occurs following high loss and high gain, rather than following negative feedback only. Third, heart rate slowing is context-dependent for negative feedback, but not for positive feedback. Heart rate slowing is more pronounced when negative feedback occurs in the context of high stakes, but not necessarily when the feedback is worse than anticipated. Fourth, heart rate responses of anxious individuals do not differ from non-anxious individuals in terms of risk anticipation. Fifth, anxious individuals show more pronounced heart rate slowing following feedback associated with high stakes,

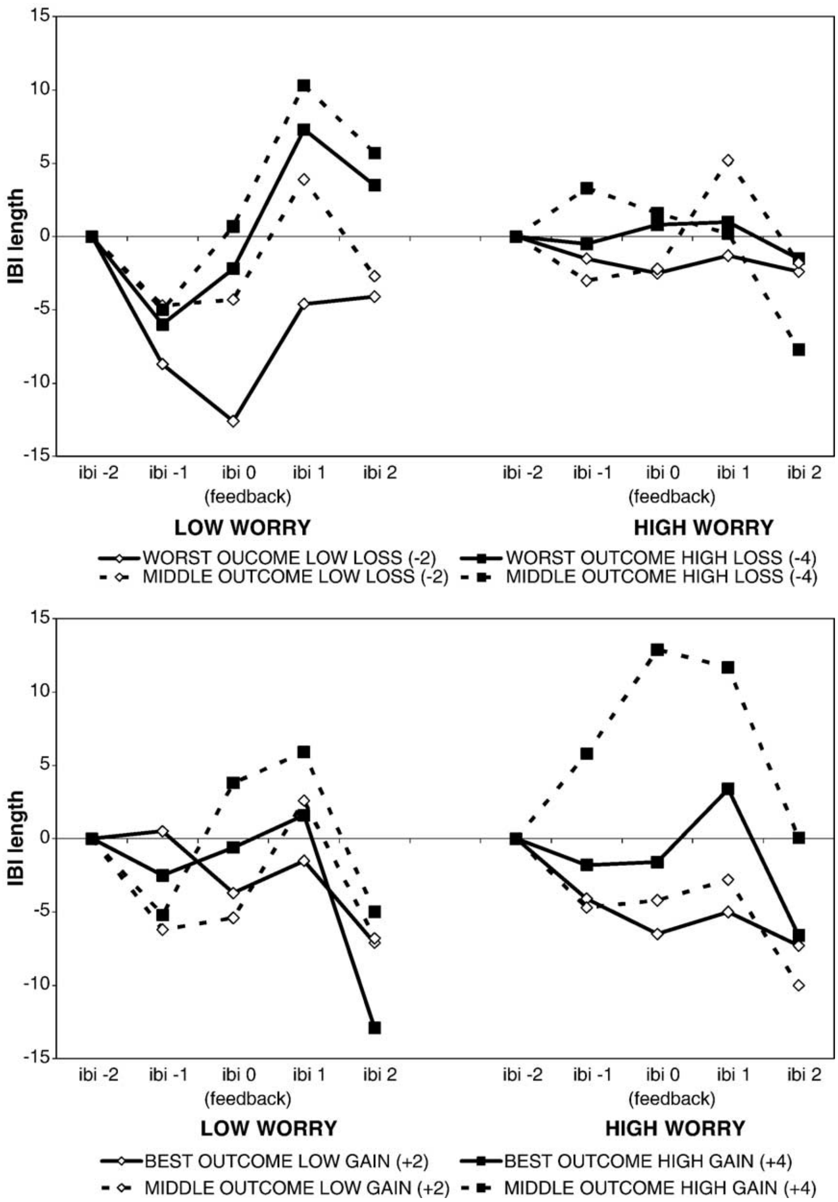

Fig. 6. Cardiac changes associated with losing 2 points or losing 4 points in Experiment 2, selected from the low-4 (worst outcome), middle-4 (intermediate outcome), middle-8 (worst outcome) and high-8 (intermediate outcome) for high and low anxiety subjects.

but do not differentiate between contexts. Below, we will discuss the implications of these findings.

11.1. Performance-related cardiac slowing

This is the first heart rate study dissociating feedback and performance. Two experiments were conducted which were similar in terms of trial types and type of feedback. The only difference between studies was that in Experiment 1, the participant had no response choices but rather had to give the same manual response to each feedback. Therefore, the participants could not influence the outcome. In Experiment 2, the participants had a response choice, and in this scenario, the participant had some influence on the outcome of the trial. A comparison of Experiments 1 and 2 shows that heart rate slowing following feedback only occurs when individuals have a response-choice.

Greater heart rate slowing has been associated with orienting and responsive engagement with the environment [27,28]. The current gambling study reveals that heart rate slows following all significant performance feedback and is not specifically related to the valence of the feedback. The valence hypothesis predicts slowing to negative feedback, even when this feedback carries no relevance to performance. In Experiment 1 of the current study, heart rate did not discriminate between positive versus negative feedback. Moreover, in Experiment 2, heart rate slowed to positive feedback when the gain was large. This finding does not support the valence hypothesis, which would predict that heart rate slows more following low gain than following high gain, because low gain is the more negative outcome.

In this respect, our findings are inconsistent with Van der Veen et al. [49]. In Van der Veen et al's experiment, participants were asked to estimate a one-second interval (following Ref. [34]). There were two conditions: an experimental condition in which positive and negative feedback was given on the basis of a performance-related threshold, and a yoked control condition in which subjects received the feedback series presented to them in the experimental condition. Thus, in the yoked control condition, the feedback was not related to the subject's actual performance. The researchers reported that heart rate slowed in response to informative (experimental condition) and uninformative (yoked control condition) negative feedback. The experiments are similar in that participants responded to stimuli with a single manual response, followed by performance feedback. The difference between the studies was that in the current study the feedback schemes were explained to the participants at the outset, whereas in Van der Veen et al.'s study participants were not aware of the yoked conditions. Thus, possibly in Van der Veen's study, participants kept trying to improve performance based on the positive and negative feedback that was given.

The results are consistent with the informative value hypothesis [10]. Following this hypothesis, the system that initiates heart rate slowing is sensitive to all events that are important for adjusting future performance, which can be events that are important for reinforcement of choices (winning) or events that are important for punishment or extinction (losing) (see also Ref. [24]).

11.2. Context sensitivity

The results suggest that the system manifested by feedback-related heart slowing operates in a context-sensitive manner; however, this effect is only seen for low anxiety individuals. Thus, for those subjects, the system determines whether an outcome is favorable or unfavorable on the basis of a range of possible outcomes. Importantly, context only affected cardiac responses to loss and not to gain. The results of Experiment 2 show that heart rate slowing is more pronounced after feedback indicating a negative outcome when there was a possibility of losing more. Thus, when the participant experiences, for example, a loss of \$5 when there was a possibility of losing \$10, then this event resulted in more pronounced heart rate slowing than when the loss of \$5 was the worst possible outcome. The finding that context did not affect gain may indicate that context is only important when there is an incentive for performance adjustment. Similar results have been reported for the feedback-ERN/MFN [15,26]. These studies showed that feedback-related brain activity following loss is different when the alternative choice would have yielded a greater loss. These results are important in showing that the system that determines the value of the outcome generally seems to operate in a context-sensitive manner.

The heart rate sensitivity to context in the current study fits with the interpretation of the informative-value hypothesis [10]. According to this hypothesis, heart rate slows following significant or meaningful events, however, there needs to be a way for the system that initiates heart rate slowing to decide which outcomes are meaningful, good or bad. The results are compelling in showing that a system that evaluates informative value, rather than valence information, initiates the heart rate slowing. This system is possibly important for appropriate performance adjustments (see also Ref. [26]).

11.3. Hypersensitive outcome monitoring in anxious individuals

The final goal of this study was to examine whether anxious individuals can be characterized by a hypersensitive or a defensive manner of processing performance feedback. The analyses focused on two aspects of performance monitoring; feedback anticipation and feedback processing. The defensive hypothesis predicted that anxious individuals would show larger cardiac slowing in anticipation of feedback that could result in high gain or loss. The hypersensitive monitoring hypothesis, in contrast, predicted that anxious individuals should be primarily hypersensitive to the actual feedback.

The results were mostly consistent with the hypersensitive monitoring hypothesis. High anxiety individuals did not differ from low anxiety individuals in terms of mean heart rate level or feedback anticipation (but see Ref. [43]). However, they showed more pronounced heart rate slowing to feedback from targets that could result in high gain or loss than low anxiety individuals. Further, low anxiety individuals showed differential heart rate slowing related to the context in which the feedback was presented, whereas high anxiety individuals showed heart rate slowing to all types of negative feedback. These findings indicate that the tuning of the system that evaluates whether feedback is informative for future performance adjustment is more responsive to informative value in low anxiety individuals. Several researchers have reported an enhanced error-related brain potential, the ERN, in individuals with high anxiety levels [14,18–20,29]. Interestingly, Hajcak et al. [19,20] reported that ERN brain activity is larger for both error trials and correct trials in high anxiety individuals. These findings are important in showing that the hypersensitive monitoring system of high anxiety individuals may not be specifically related to errors, but may indicate that the high anxiety group doubts and checks all significant actions, regardless of whether or not a mistake is actually made (cf. Refs. [19,20]).

The current results are inconsistent with the defense-response hypothesis suggested by Thayer et al. [44]. These researchers compared cardiac changes of anxious and non-anxious individuals in a paradigm in which participants received neutral cues followed by threat and non-threat stimuli. Individuals with high anxiety levels showed smaller orienting responses and impaired habituation to neutral words followed by threat stimuli. Anxious individuals also showed increased anticipatory heart rate slowing to the threat words. In contrast, control individuals exhibited fast habituation to neutral and threatening words [44]. The increased heart rate acceleration to threat words in anxious individuals was presumed to reflect an attempt to shield against the impact of threat, similar as seen in phobic individuals [22]. We did not observe anticipatory differences between low and high anxiety individuals in the current experiment.

When individuals are anticipating a negative event, heart rate typically accelerates (Somsen et al., 1983), a response associated with directing attention internally [30,31]. Possibly, the anxious participants in Thayer et al.'s study showed a preattentive emotional bias towards threat. The heart rate slowing associated with performance outcomes in the current study seems more associated with a mechanism which is involved when there is a need to check outcomes for the purpose of adjusting future actions (see Ref. [39]).

11.4. Neural systems associated with heart rate slowing

The present study demonstrated that the system that initiates heart rate slowing bases its evaluations on the value of possible outcomes in the task, rather than the absolute value of gain or loss. This result is consistent with a reinforcement learning model reported in the literature [24], according to which ACC evaluates ongoing events, including performance feedback, and predicts whether events will be favorable or unfavorable for the purpose of adjusting subsequent actions. The systems giving rise to the error-related cortical negativity and heart rate slowing may share the same neural substrates. Recent progress in the study of the central control of heart rate modified earlier concepts that attributed autonomic control primarily to brainstem nuclei. Areas that alter cardiac function were the medial prefrontal cortex, ACC, the insula, the temporal pole, and some limited areas in primary sensory and motor cortex [7]. These sites, identified primarily in animals, have more recently been verified in human brain imaging work and continued work with patients with brain lesions (e.g., [8,9,37,40]). For example, the cingulate gyrus has been related to error-related negativity using source localization techniques, and has also been identified using functional magnetic resonance imaging in tasks requiring performance monitoring [5,25]. Imaging work further suggests that the caudal portion of this structure may be related more to cognitive monitoring, while the affective aspects of such error identification might involve the rostral portion of this structure [51]. The rostral cingulate is also known to connect to midbrain circuitry related to autonomic control. These results then lead to the strong hypothesis that heartbeat slowing is influenced by rostral cingulate structures.

Studies that have investigated the biological mechanisms associated with excessive anxiety or worrying have reported that increased performance monitoring may be associated with increased ACC activity [14,18–20]. Anxiety is often associated with somatic complaints and increased heart rate variability [44]. The current study shows that somatic differences are also reflected in phasic cardiac changes associated with performance monitoring.

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