



# Attention and anticipation in response to varying levels of uncertain threat: An ERP study

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## Abstract

Individual differences in responding to uncertainty have been proposed as a key mechanism of how anxiety disorders develop and are maintained. However, most empirical work has compared responding to uncertain versus certain threat dichotomously. This is a significant limitation because uncertainty in daily life occurs along a continuum of probability, ranging from very low to high chances of negative outcomes. The current study investigated (1) how varying levels of uncertainty impact attention and anticipatory emotion, and (2) how these effects are moderated by individual differences in risk factors for anxiety disorders, particularly intolerance of uncertainty (IU) and worry. Participants ( $n = 65$ ) completed a card task in which the probability of shock varied across trials. Two event-related potential components were examined: the P2, an index of attention, and the stimulus-preceding negativity (SPN), an index of anticipation. The P2 tracked the level of uncertainty and was smaller for more uncertain outcomes. Participants higher in IU exhibited greater differences in the P2 across levels of uncertainty. The SPN did not track specific levels of uncertainty but was largest for uncertain threat compared with certain threat and safety. Greater worry was associated with blunting of the SPN in anticipation of all outcomes. Thus, attention appears to be sensitive to variations in uncertainty, whereas anticipation seems sensitive to uncertainty globally. The two processes appear to be distinctly related to anxiety risk factors. These results highlight the value of examining multiple aspects of anticipatory responding to varying levels of uncertainty for understanding risk for anxiety disorders.

**Keywords** Anticipation · Attention · Uncertainty · Intolerance of uncertainty · Worry · Anxiety · SPN · P2

Uncertainty is ubiquitous. In many everyday situations, such as driving to work, we cannot be absolutely certain of what the outcome will be—will we make it on time, will traffic delay us, or will we be in a horrible car accident? The uncertainty that characterizes daily life can be distressing and elicits a host of anticipatory cognitive, affective, and behavioral responses, such as worry, anxiety, and avoidance (Grupe & Nitschke, 2013). Individuals with and at risk for anxiety disorders report finding uncertainty especially distressing and intolerable and

show excessive anticipatory responses such as worry when faced with uncertain situations (Grillon, 2008). Thus, individual differences in responding to uncertainty may play an important role in understanding risk for anxiety disorders.

Recent models of anxiety disorders highlight the importance of examining early attentional processes and anticipatory emotional reactivity in the face of uncertain threat (Grupe & Nitschke, 2013). When encountering an uncertain situation, attention may be deployed to information in the environment in order to disambiguate the uncertainty (Pearce & Hall, 1980; Peters, McEwen, & Friston, 2017). While awaiting the uncertain outcome, one also has an anticipatory emotional response (Barlow, 2004; Grillon, 2008). Excessive deployment of attention and intense anticipatory emotion in the face of uncertainty have been hypothesized to be two key mechanisms by which clinical anxiety develops and is maintained (Grupe & Nitschke, 2013). Numerous studies have suggested that attention, as indexed by measures like eye gaze and event-related potentials (ERPs), is enhanced in uncertain contexts—especially among participants who report greater anxiety

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(Dieterich, Endrass, & Kathmann, 2016; Koenig, Uengoer, & Lachnit, 2017; Nelson, Hajcak, & Shankman, 2015). Similarly, a wealth of research has demonstrated that anticipatory emotion, as indexed by measures like peripheral psychophysiology, is enhanced under conditions of uncertain threat compared with certain threat (for a review, see Grillon, 2008). Again, these effects are greater among those with anxiety disorders (Gorka, Lieberman, Shankman, & Phan, 2017) and higher levels of anxiety-related traits (Chin, Nelson, Jackson, & Hajcak, 2016).

However, a key limitation of this work is that most studies examining the effects of uncertainty on attention and anticipatory emotion focus on the comparison of uncertain versus certain threat dichotomously. As a consequence, the differential effects of varying levels of uncertainty on attention and anticipatory emotion remain unknown. This is problematic because daily life is characterized by varying probabilities of uncertain outcomes. For example, imagine driving to an important meeting that one does not want to be late for. Uncertainty could be low (“I have a reserved parking spot that I expect to be able to park in”), moderate (“The department shares a parking lot where I can often find a spot”), or high (“I hope to find street parking”). Determining at which levels of uncertainty those at risk for anxiety show elevated attention and anticipatory emotion may have important implications for understanding the development of anxiety disorders and the situations in which anxious individuals are most likely to respond intensely. While anxious reactions in the face of very high levels of uncertainty are considered to be normative and even adaptive (Carleton, 2012), anxiety in the face of low levels of uncertainty is hypothesized to be associated with risk for anxiety disorders (e.g., “I must get away from *all* uncertain situations.”; Buhr & Dugas, 2002, italics added). This conceptualization suggests that high-risk individuals differ from those who are at a low-risk particularly at very low levels of uncertainty, but this proposition has not been empirically tested. To understand risk for anxiety disorders, it is thus imperative to study anticipatory responding to uncertainty ranging from very low to very high levels of uncertain threat.

No work thus far has examined the effects of varying levels of uncertainty on attention, but some recent studies suggest that specific levels of uncertainty may have distinct effects on anticipatory emotion. For example, the dampening effects of alcohol on startle responses to threat are greatest when there is a 20% chance of shock, followed by 60%, followed by 100% (Hefner & Curtin, 2012). Additionally, a 75% chance of threat elicits greater startle responses than a 50% chance of threat (Chin et al., 2016). Other work examining skin conductance responses (SCRs) has found that a 66% chance of shock elicits greater responses than a 33% chance (Chandrasekhar, Capra, Moore, Noussair, & Berns, 2008). However, all of these studies only examined two probabilities of uncertain threat, thus providing only a portion of the full picture of responses to

uncertainty. Recent work by Ring and Kaernbach (2015) suggests that SCRs track increases in the probability of a threat, such that higher SCRs are elicited for threat that is more likely. However, these authors only varied threat probability between 0 and 50%, so uncertainty and threat were confounded—as threat probability increased, so did uncertainty. It thus remains unclear what the effects of varying levels of uncertainty on indices of anticipatory emotion are.

The current study used a card game task adapted from Ring and Kaernbach (2015), in which the participant plays a rigged card game against the computer. On each trial, the goal is to select a higher card than the computer’s, and if the participant loses, they have a chance of being shocked. Probability of threat varies based on the value of the card the participant draws (which is not chosen by the participant but is instead predetermined at the start of each trial). Our version of the task included two important modifications. First, certain threat and certain safety conditions were incorporated, so that a full range of levels of uncertainty (0% to 100% chance of electric shock) could be examined. Second, the task was modified for use with ERPs. Because of their temporal resolution, ERPs allow for the examination of multiple stages of responding over the course of a single trial—specifically, attention and anticipatory emotion were examined. Attention to information about uncertainty was investigated by examining neural activity immediately following presentation of stimuli that denoted varying levels of threat uncertainty. The P2 is an early ERP component that is elicited approximately 200 ms following a visual stimulus and is thought to reflect selective attention that occurs following initial perceptual processing (Hajcak, Weinberg, MacNamara, & Foti, 2011). Previous work has shown that the P2 is enhanced by threat (Rossignol, Campanella, Bissot, & Philippot, 2013) and uncertainty (Dieterich et al., 2016). We examined whether the P2 varied based on the level of uncertainty denoted in each trial.

To examine anticipatory emotion in the face of uncertainty, the stimulus preceding negativity (SPN) was examined. The SPN is a slow cortical potential that is elicited when anticipating an outcome (Hajcak et al., 2011). The SPN is enhanced by negative emotion (Böcker, Baas, Kenemans, & Verbaten, 2001) and uncertainty in paradigms where outcomes are neutral (Catena et al., 2012), rewarded (Foti & Hajcak, 2012) and threatening (Seidel et al., 2015). We examined whether the SPN in the 200 ms leading up to the revelation of the trial outcomes varied based on the level of uncertainty. It was hypothesized that both the P2 and SPN would increase as uncertainty increased, such that the largest amplitudes would be observed for the most uncertain stimuli. Thus, we expected uncertain threat to elicit greater modulation of the P2 and SPN than certain threat.

The second central goal of the current study was to examine whether neural responses to uncertainty are moderated by individual differences in risk for anxiety. Both intolerance of

uncertainty (IU) and worry are constructs that represent negative reactions to uncertainty and that have been closely linked to risk for anxiety (Crouch, Lewis, Erickson, & Newman, 2017; McEvoy & Mahoney, 2012; Oglesby, Boffa, Short, Raines, & Schmidt, 2016; Young & Dietrich, 2015). IU refers to the tendency to find uncertainty aversive and threatening (Carleton, 2012), and worry is a style of future-oriented, repetitive negative thought that represents an attempt to reduce uncertainty by considering every possible outcome of an uncertain situation (Dugas, Buhr, & Ladouceur, 2004). It was hypothesized that IU would be associated with greater initial attention to stimuli conveying information about uncertain threat, reflected in the P2. Further, IU was expected to be associated with higher levels of anticipatory emotion, reflected in the SPN, when anticipating uncertain threat. No relation between worry and the P2 was expected; because the P2 is a very early attentional process, the reflective and elaborative nature of worry was not expected to influence early attention above and beyond IU. Because of the ineffectiveness of worry as an emotion regulation strategy (e.g., Skodzik, Zettler, Topper, Blechert, & Ehring, 2016; Young & Dietrich, 2015), it was hypothesized that worry would be associated with enhancement of the SPN independently of IU.

Importantly, the measure most often used to examine IU, the Intolerance of Uncertainty Scale (IUS), consists of two factors: prospective IU, which refers to desire for predictability and active seeking of certainty, and inhibitory IU, which refers to paralysis of cognition and action in the face of uncertainty (Carleton, 2012). Prospective IU has been shown to be more associated with generalized anxiety disorder and obsessive-compulsive disorder, while inhibitory IU is more associated with social anxiety disorder, panic disorder, and depression (McEvoy & Mahoney, 2012). Because the two factors show differential relations with psychopathology, the current study took an exploratory approach to examine whether prospective and inhibitory IU differentially relate to attention and anticipatory emotion in the face of uncertainty.

## Method

### Participants

Sixty-five members of the community (34 female) were recruited via electronic and print advertisements. The sample size was determined based on previous work and a power analysis. Because the study used a paradigm similar to that of Ring and Kaernbach (2015), we relied on their data for estimates of the basic task effects; their sample consisted of 32 individuals. Because the current study also investigated individual differences, we conducted a power analysis with an estimated effect size based on previous findings regarding ERPs and psychopathology-related individual differences

(e.g., Moser, Moran, Schroder, Donnellan, & Yeung, 2013), which suggested a sample of 61 at  $\beta = 0.80$ .

Five participants were excluded from further analysis because more than 25% of trials in one or more conditions contained artifacts that compromised the quality of the EEG data. One participant was excluded due to issues during EEG recording. The final sample consisted of 59 participants (32 female) with a mean age of 26.67 years ( $SD = 7.68$ ). Of these participants, 61% identified as White/Caucasian, 13.56% as Asian, 8.47% as Latino/Latina, 8.47% as Black/African American/African and 8.47% as more than one race. The Yale University Human Subjects Committee approved the study, and informed consent was obtained from each participant prior to beginning the procedure. Participants were compensated \$15.00 per hour for their time. No participants chose to discontinue their participation.

### Measures

**Intolerance of Uncertainty Scale (IUS-12)** The IUS is 12-item self-report questionnaire that measures dislike of and reactions to uncertainty (Carleton, Norton, & Asmundson, 2007). It is an abbreviated version of the original 27-item measure, with which it is highly correlated (Carleton et al., 2007; Freeston, Rhéaume, Letarte, Dugas, & Ladouceur, 1994). Participants rate items on a 5-point scale (from *not at all characteristic of me* to *entirely characteristic of me*). In the current sample, the IUS had high internal consistency ( $\alpha = .87$ ), as did the prospective ( $\alpha = .82$ ) and inhibitory ( $\alpha = .78$ ) subscales.

**Penn State Worry Questionnaire (PSWQ)** The PSWQ (Meyer, Miller, Metzger, & Borkovec, 1990) was used to assess worry. On a 5-point scale, participants rated their agreement with 16 items that examine the degree to which an individual's worry is excessive, generalized, and uncontrollable. The PSWQ had high internal consistency ( $\alpha = .91$ ).

### Card-game task

The card-game task, adapted from work by Ring and Kaernbach (2015), consisted of four blocks of 36 trials each and lasted approximately 40 minutes.<sup>1</sup> All participants completed three practice trials in which they experienced both a loss and a win trial. Participants were told they would be playing a card game against the computer in which the goal is to choose a higher card than the computer. In each round, participants saw 10 cards face-down on the screen. They were told that the cards were numbered one through 10, in addition

<sup>1</sup> Some participants ( $n = 7$ ) completed only three blocks due to time constraints during the EEG recording session.

For these participants, 108 trials were collected instead of 144.

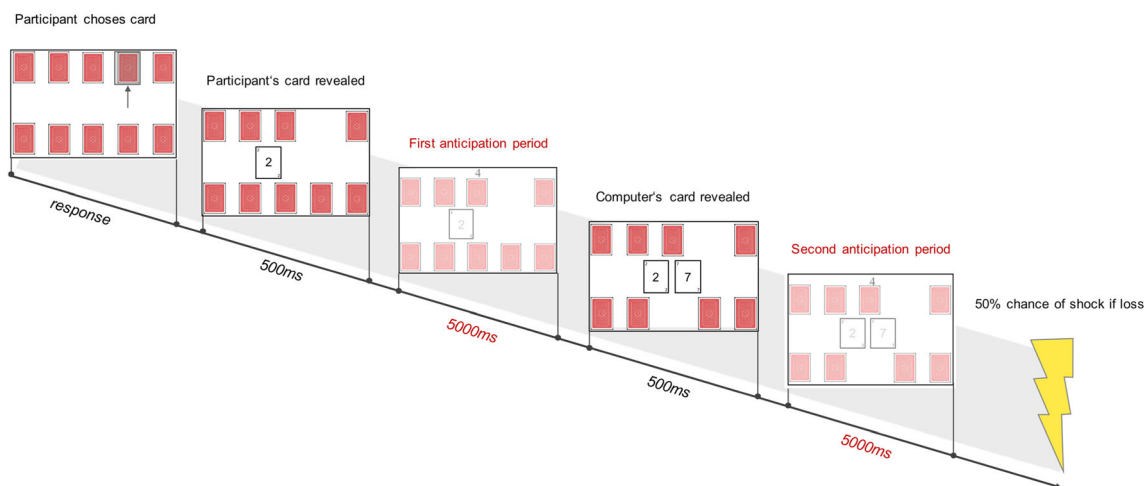
to two special cards, described below. Using a keyboard, participants selected one of the face-down cards, and the value of the card was revealed. Although participants were able to choose any card on the screen, the value of their card was predetermined at the start of every trial. After selecting a card, they viewed a countdown while waiting for the computer to choose and reveal its card; this was the first anticipation period, and it lasted 5 seconds. Once the computer's card was revealed, participants knew whether their card, also displayed on the screen, was higher or lower and thus whether they had won or lost. Every time they lost, they had a 50% chance of receiving an electric shock. After the computer's card was revealed, another countdown appeared, at the end of which participants either received a shock or the trial ended; this was the second anticipation period, and it lasted 5 seconds. At the end of the trial, participants were asked whether they won or lost in order to ensure that they remained attentive. Participants could never tie with the computer; they were instructed that there was only one card of each value in a given round. An example trial is shown in Fig. 1. Each trial began with a new set of 10 face-down cards on the screen, and the cards were drawn with equal frequency (exact numbers of trials per condition are reported below).

The uncertainty of the first anticipation period varied based on the value of the participant's card on a given trial. For example, if the participant's card was a 10, the participant could be sure that he or she would win the round. If the card was a five, he or she would know that the probability of losing the round was 50%. If the card was a one, he or she would know that the probability of losing was 100%, and so on. In this way, the first anticipation period

allowed for the examination of responses to 10 different levels of uncertainty.

In order to have a condition that signifies certain shock, one card with a lightning bolt was "in the deck." When drawn, this card indicated that the participant would definitely receive a shock at the end of the trial, no matter which card the computer drew. To avoid having more loss than win trials with the addition of the certain shock card, a card with a lightning bolt with a red line through it was also included. When drawn, this card indicated that the participant would not receive a shock at the end of the trial, no matter which card the computer drew. When the participant drew either of the special cards, the computer simply drew a blank card. The computer itself never drew a special card. These cards were included in the design of the task in order to allow for a certain threat condition in the second anticipation period.

During the second anticipation period, after both the participant and computer's cards were revealed, there were three possible levels of uncertainty: a 50% chance of being shocked if the participant lost, a 0% chance of being shocked if the participant won, and 100% chance of being shocked if the participant drew the certain shock card. The second anticipation period allowed for the examination of responses to uncertain threat compared to certain threat and safety. In addition to examining responses to varying levels of uncertain threat, the design included the second anticipation period to allow for a simple test of the effects of uncertainty versus certainty in a binary manner. This was especially important for examining the SPN, as no work thus far has compared the SPN in anticipation of uncertain threat versus certain threat.



**Fig. 1** Diagram of the card-game task. Participants see 10 cards face-down on the screen. They are then able to select one, the value of which is immediately revealed. Then, participants view a 4-second countdown (the total duration of which is 5,000 ms including the final 1,000 ms between the display of the "1" and the revelation of the computer's card). This constitutes the first anticipation period. The computer's card is then revealed. Then, participants view another 4-second countdown (the total

duration of which is also 5,000 ms, including the final 1,000 ms between the display of the "1" and the potential delivery of the shock). This constitutes the second anticipation period. If they lost, a shock is delivered 50% of the time; if they won, the trial ends. At the end of the trial, participants are asked whether they won or lost in order to ensure that they are remaining attentive. (Color figure online)



## Shock set-up and calibration

Electric shocks were administered to the median nerve of the nondominant wrist using two Ag/AgCl electrodes positioned 20 mm apart. Shocks were delivered using a Grass Instruments stimulator (Grass Instruments, Quincy, MA, USA), which is isolated from the ground and was developed for research; its use to administer mild electric shocks does not present any risks to participants beyond mild discomfort.

Prior to beginning the card-game task, the intensity of the shocks was calibrated individually for each participant. Calibration was done by first delivering a shock of low intensity, 10 V, and increasing the voltage by 5 V with every subsequent shock and with the participant's permission. The voltage of shocks never exceeded 60 volts.<sup>2</sup> Participants were told that the goal was to reach a level that they found uncomfortable and unpleasant, but not painful.

Specifically, the experimenter verbally provided a scale from 1 to 5 for rating the shocks, where 1 was *not noticeable*, 2 was *hardly noticed*, 3 was *acceptable*, 4 was *unpleasant/uncomfortable*, and 5 was *painful*.<sup>2</sup> The experimenter informed the participant that the target intensity was 4—unpleasant/uncomfortable, but reminded the participant that he or she could select whatever intensity he/she was comfortable with and could stop anytime. After participants decided on a particular voltage, they rated the intensity of the shock using the aforementioned rating scale on the computer. After completing the card-game task, participants once again rated the intensity of the shocks overall.

## Electrophysiological recording and data processing

Electroencephalography activity was recorded using a 64-channel cap (Quik-Cap, Compumedics Neuroscan, Eaton, OH, USA) with Ag/AgCl electrodes arranged based on the 10–20 system. Electrodes were placed on the left and right mastoids; during off-line processing, all data were referenced to the average of these channels. Eye movements and blinks were recorded from four electrodes placed around the right and left eyes. One electrode was placed one centimeter outside of each eye to record horizontal eye movements. Electrodes were also placed above and below the left eye to record vertical eye movements. Data were recorded using a Neuroscan Synamps2 amplifier and acquisition software (Compumedics, Charlotte, NC, USA). The impedance of all electrodes was reduced to 5 K $\Omega$  or below using conductive gel and light abrasion.

The EEG data were digitized at a sampling rate of 2500 Hz with a digital high-pass filter of 0.05 Hz. Off-line processing

was done using BrainVision Analyzer (Brain Products GmbH, Munich, Germany). A second-order Butterworth zero-phase low-pass filter with half-power cutoff of 20 Hz was applied. To examine the first anticipation period, data were segmented into stimulus-locked epochs that included 500 ms before the participant's card was revealed and the 5,000 ms leading up to the revelation of the computer's card. To examine the second anticipation period, data were segmented into stimulus-locked epochs that included the 5,000 ms leading up to the end of the trial. Ocular corrections were performed using the Gratton and Coles algorithm (Gratton, Coles, & Donchin, 1983). Artifacts were detected and rejected through semiautomatic inspection. Segments falling outside of the following parameters were automatically marked for rejection: a maximal voltage step of 50  $\mu$ V/ms, a maximal difference of 300  $\mu$ V between the highest and lowest points in an interval of 200 ms, and activity below 0.5 $\mu$ V for 100ms. Additional artifacts not already detected were manually removed.

For the first anticipation period, trials were segmented based on which card was revealed (i.e., the anticipation periods following each value—1 through 10, as well as the certain shock and certain safety—were separated). For the second anticipation period, trials were segmented based on whether the participant had won, lost, or drawn the certain shock card. Each channel for each trial type was averaged across all of the trials, to yield one average for each channel for each trial type. For each of the cards numbered one through 10, as well as the certain shock and certain safety cards, 12 trials comprised the average for the first anticipation period. For the second anticipation period, there were 12 certain threat trials (i.e., the certain shock card), 60 uncertain trials (i.e., all trials on which the participant lost and thus had a 50% chance of shock), and 72 certain safe trials (i.e., the certain safety card and all trials on which the participant won). It is important to note that mean amplitudes were calculated for the components, described below, thus not risking bias that could occur for peak amplitudes due to having different numbers of trials per condition (Luck, 2014, pp. 143, 289). For analyses of the P2 and SPN in the first anticipation period, the 500-ms interval before the participant chose a card served as the baseline.

For analyses of the SPN in the second anticipation period, the period 1,000 to 2,000 ms after the computer's card was revealed served as a baseline. This period was chosen because early processing of the card stimulus was expected to be completed by 1,000 ms, and it was expected that anticipation would not differ between conditions so early into the anticipation period, as reflected in the waveform figures below.

Based on visual inspection of the grand average waveform for all participants across conditions, a positive potential peaking at approximately 200 ms following revelation of the participant's card was observed; the timing and topography appeared consistent with that of the P2. The P2 was measured as the mean activity in the 150 to 300 ms

<sup>2</sup> Due to experimenter error, one participant was allowed to choose a shock level of 65 volts.

following the revelation of the participant's card at midline electrode sites, Fz, FCz, Cz, and CPz. The SPN in the first anticipation period was calculated as the mean activity in the 200 ms preceding the revelation of the computer's card at frontal electrode sites where the SPN was found to be maximal: Fz, F1, and F2. Because the first anticipation period featured 10 numbered cards (i.e., Card 1 through Card 10) that denoted distinct levels of threat uncertainty, the P2 and SPN were examined separately for each. The P2 and SPN are also reported for the two special cards that denoted certain shock and certain safety, but the amplitudes for these two conditions are not included in the first anticipation period analyses for two reasons. First, they differed substantially in their visual properties from Cards 1 through 10, which would introduce a potential confound for the P2. Second, they differed in how much attention they would elicit from the participant during the latter part of the first anticipation period; after drawing the certain shock or safety cards, participants no longer needed to pay attention until the second anticipation period because they had been told that the computer's card would be blank. Thus, this difference would introduce a potential confound for the SPN. However, the values for the P2 and SPN in response to the certain shock and safety cards are reported and displayed in the figures for informational purposes. Additional exploratory analyses for the first anticipation period are reported in the [Supplementary Materials](#).

The SPN in the second anticipation period was calculated as the mean activity in the 200 ms preceding the end of the trial, when a shock could either be delivered or not, at electrode sites Fz, F1, and F2. The second anticipation period was characterized by three levels of threat uncertainty: a 50% chance of shock, a 100% chance, and a 0% chance. The SPN was examined separately for each condition.

## Results

### Self-report data

The mean score on the IUS was 27.53 ( $SD = 9.07$ ; possible score range: 12–60), with a mean score on the prospective subscale of 18.24 ( $SD = 5.82$ ; possible score range: 7–35) and a mean score of 9.29 on the inhibitory subscale ( $SD = 4.11$ ; possible score range: 5–25). The mean score on the PSWQ was 48.02 ( $SD = 11.68$ ; possible score range: 16–80). Intolerance of uncertainty and worry were significantly correlated,  $r = .63$ ,  $p < .001$ . The prospective and inhibitory subscales were significantly correlated with each other,  $r = .66$ ,  $p < .001$ , and with the PSWQ (prospective subscale:  $r = .49$ ,  $p < .001$ ; inhibitory subscale:  $r = .71$ ,  $p < .001$ ).

### Shock calibration

Participants chose shock levels that ranged from 20 to 65 volts ( $M = 45.34$ ,  $SD = 11.55$ ). All participants rated the shocks as a 3 (*acceptable*) or 4 (*unpleasant*) when asked immediately after the shock calibration, before the card-game task ( $M = 3.86$ ,  $SD = 0.35$ ). When asked for a second time after completing the card-game task, all participants again rated the shocks as either a 3 or 4 ( $M = 3.48$ ,  $SD = 0.50$ ). The second rating was significantly lower than the first rating,  $t(26) = 4.92$ ,  $p < .001$ , indicating that participants habituated to the shocks.

However, the magnitude of this habituation was small, and all participants' evaluations of the shocks remained in the desired range (of 3 to 4). IUS and PSWQ scores were unrelated to the chosen intensity of the shock ( $r = .05$ ,  $p = .72$ ;  $r = -.03$ ,  $p = .81$ , respectively), the initial rating of the shock ( $r = -.03$ ,  $p = .84$ ;  $r = -.12$ ,  $p = .37$ , respectively), and the second rating of the shock ( $r = -.16$ ,  $p = .22$ ;  $r = -.02$ ,  $p = .89$ , respectively).

### Behavioral data

On average, participants selected a card in 2.10 seconds ( $SD = 1.00$ ).<sup>3</sup> They won approximately 48.78% of trials ( $SD = 0.03$ ) and received an average of 11.14 shocks per block ( $SD = 1.24$ ). To ensure that participants understood that they would receive shocks in each block, the first loss trial of each block always resulted in a shock.

### Electrophysiological data

The mean amplitude of the P2 in the first anticipation period, when participants anticipated whether they would win or lose on that trial, is depicted in Fig. 2, along with the waveforms for every card value. To investigate whether attention is sensitive to varying degrees of uncertainty, the P2 following the revelation of each card was examined.<sup>4</sup> A repeated-measures ANOVA revealed that the P2 significantly differed across cards 1 (0% chance of loss) through (100% chance of loss),  $F(4.72, 273.76) = 8.32$ ,  $p < .001$ ,  $\eta_p^2 = .13$ .<sup>5</sup> Specifically, the effect was quadratic,  $F(1, 58) = 73.64$ ,  $p < .001$ ,  $\eta_p^2 = .56$ , indicating that the P2 is sensitive to variations in uncertainty and, contrary to

<sup>3</sup> Reaction time on the first trial of each block was excluded because participants were required to wait for the experimenter to permit them to begin.

<sup>4</sup> The pattern of results across all of the analyses of the P2 is the same when the certain shock and certain safety cards are included.

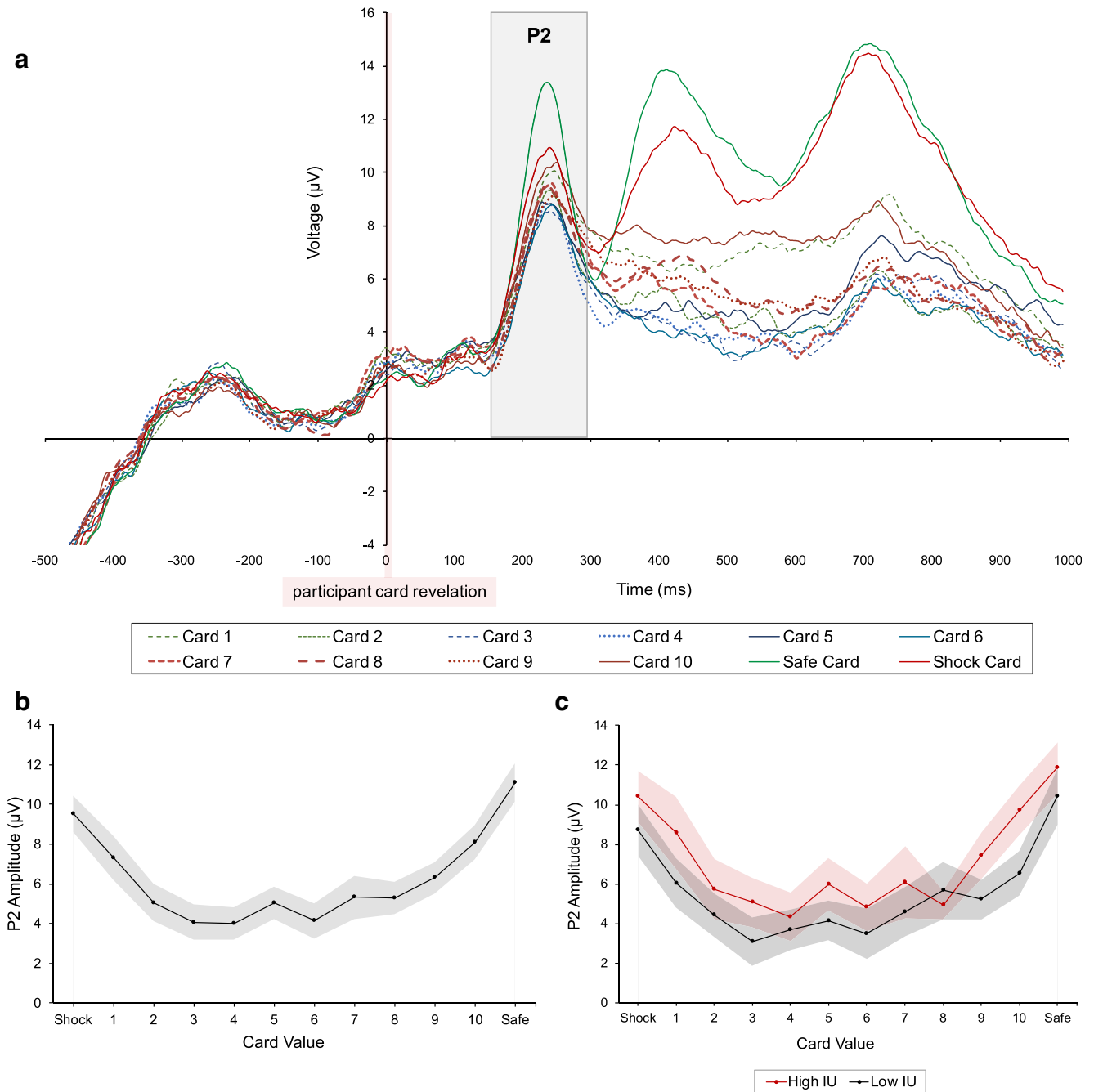
<sup>5</sup> Because Mauchly's test of sphericity indicated that the assumption of sphericity was violated,  $\chi^2(44) = 137.03$ ,  $p < .001$ , the reported statistics for the repeated-measures ANOVA examining the effect of uncertainty on the P2 refer to Greenhouse–Geisser-corrected values.

what was hypothesized, is smaller for more uncertain stimuli.

To examine whether IU moderated the effect of uncertainty on the P2, the total score on the IUS was included as a covariate in the model. A significant interaction between IU and change in the P2 across levels of uncertainty emerged,  $F(4.86, 276.72) = 2.30, p = .047, \eta_p^2 = .04$ . A median split, shown in Fig. 2, revealed that individuals higher in IU had a

stronger quadratic effect of uncertainty on the P2 than did those lower in IU.

To explore whether the moderating effects of IU on attention differ across the prospective versus inhibitory subscales of the IUS, the prospective and inhibitory subscales were separately included as covariates in the repeated-measures ANOVA examining the effect of uncertainty on the P2. A significant interaction between inhibitory IU and change in



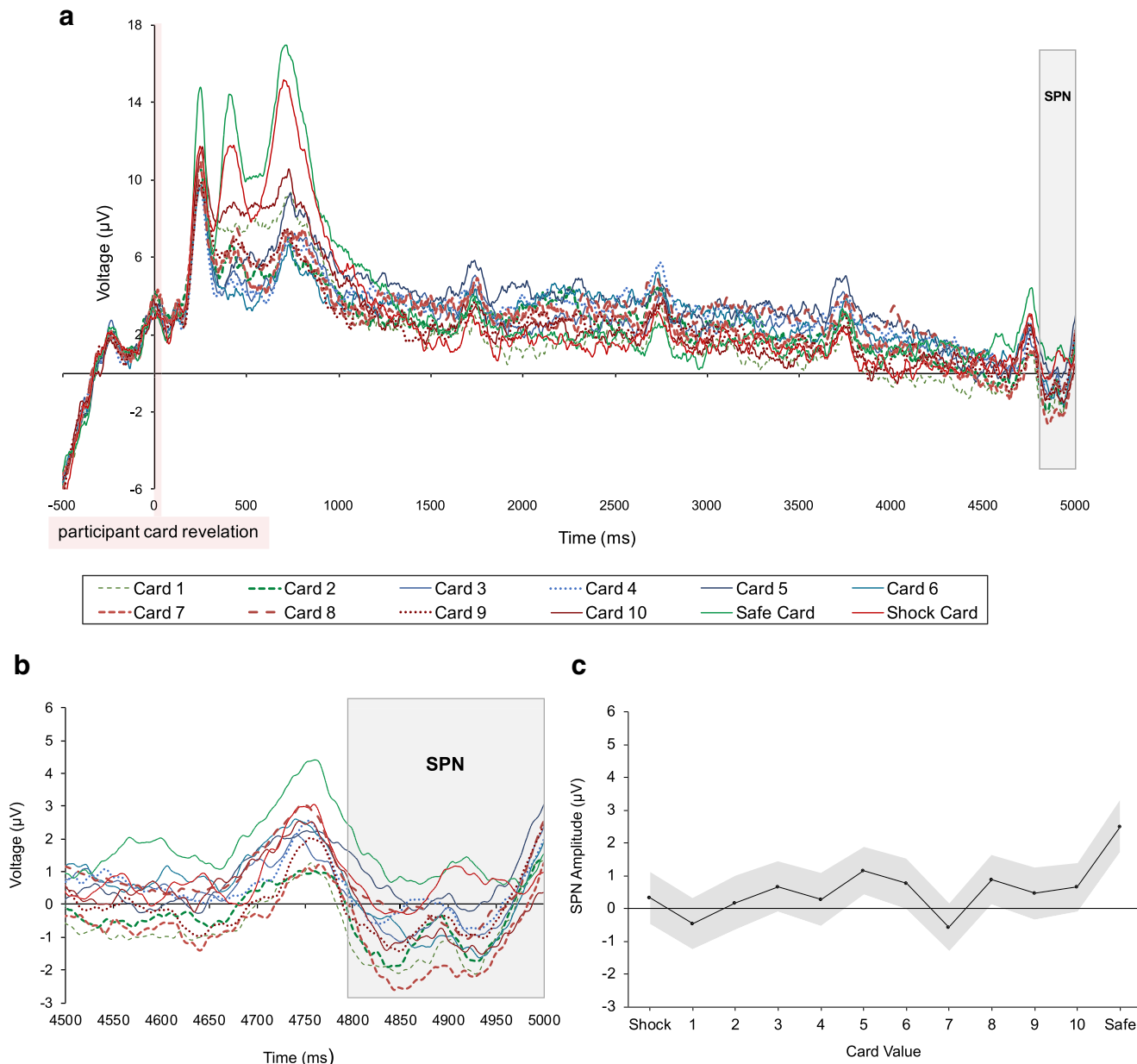
**Fig. 2** Activity time-locked to the presentation of the card in the first anticipation period at Fz, FCz, Cz, and CPz. a The P2 was calculated in the interval of 150–300ms following the revelation of the participant’s card. Baseline correction was done using the 500-ms interval immediately

preceding the revelation of the card. b Mean amplitude of the P2 in the first anticipation period for every card value. c A median split showing the effect of uncertainty on the P2 among those with high and low scores on the Intolerance of Uncertainty Scale. (Color figure online)

the P2 across levels of uncertainty emerged,  $F(4.93, 281.24) = 2.73, p = .02, \eta_p^2 = .05$ , paralleling the results using the total IUS score as a covariate. When the prospective IU subscale was examined, a significant main effect emerged,  $F(1, 57) = 4.61, p = .04, \eta_p^2 = .08$ , such that individuals higher in prospective IU exhibited larger P2 amplitudes. Figures depicting median splits of prospective and inhibitory IU are included in the [Supplementary Materials](#). The results of this exploratory analysis indicate that the two subscales of the IUS have differential moderating effects on the relation between uncertainty and attention.

To examine whether worry moderated the effect of uncertainty on the P2, the total score on the PSWQ was included as a covariate in the repeated-measures ANOVA examining P2 magnitude across the 10 card values. Worry did not have a significant main effect,  $F(1, 57) = 0.20, p = .89, \eta_p^2 < .001$ , or interaction,  $F(4.65, 265.28) = 0.99, p = .42, \eta_p^2 = .02$ .

The mean amplitude of the SPN in the first anticipation period, when participants anticipated whether they would win or lose on that trial, is depicted in Fig. 3, along with the waveforms for every card value. To investigate whether anticipatory emotion is sensitive to varying degrees of uncertainty,



**Fig. 3** Activity time-locked to the presentation of the card in the first anticipation period at Fz, F1, and F2. **a** The SPN was calculated in the 200 ms preceding the outcome of card game (i.e., whether the computer’s card was lower or higher). Baseline correction was done using the interval

of 1,000 to 2,000 ms following the revelation of the computer’s card. **b** Zoomed-in waveform of the SPN. **c** Mean amplitude of the SPN in the first anticipation period for every card value. (Color figure online)



the SPN following the revelation of each card was examined.<sup>6</sup> There were no significant differences in the magnitude of the SPN elicited in the first anticipation period based on the value of the participant's card,  $F(9, 513) = 0.89, p = .53, \eta_p^2 = .02$ , indicating that the SPN does not seem to track specific levels of uncertainty. To examine whether the effect of uncertainty on the SPN differed based on individual differences in IU, the total score on the IUS was included as a covariate in the repeated-measures ANOVA examining the SPN across the 10 card values. IU did not have a significant main effect,  $F(1, 57) = 0.04, p = .85, \eta_p^2 = .001$ , or interaction,  $F(9, 513) = .45, p = .91, \eta_p^2 = .01$ . Worry also did not have a significant main effect,  $F(1, 57) = 0.04, p = .85, \eta_p^2 = .001$ , or interaction,  $F(9, 513) = 1.20, p = .29, \eta_p^2 = .02$ .

In the second anticipation period when participants awaited whether or not they would be shocked, the SPN preceding the outcome of the trial—a 50% chance of shock, a 100% chance of shock, or a 0% chance of shock—was examined to investigate whether anticipatory emotion is sensitive to uncertain threat broadly relative to certain threat and safety. The mean amplitude of the SPN in the second anticipation period is depicted in Fig. 4, along with the waveforms for each of the three conditions. The SPN preceding uncertain threat ( $M = -2.06, SD = 4.04$ ), certain threat ( $M = -0.81, SD = 4.55$ ), and safety ( $M = -0.34, SD = 3.28$ ) significantly differed,  $F(2, 116) = 4.93, p = .01, \eta_p^2 = .08$ . A follow-up  $t$  test revealed that the SPN preceding uncertain threat was significantly larger (i.e., more negative) than the SPN preceding certain threat,  $t(58) = -2.11, p = .04$ . To examine whether IU moderated the effect of uncertainty on the SPN, the total score on the IUS was included in the model as a covariate. IU did not have a significant main effect,  $F(1, 57) = 1.48, p = .23, \eta_p^2 = .03$ , or interaction,  $F(1, 57) = 1.48, p = .23, \eta_p^2 = .03$ . On the other hand, when worry was included as a covariate in the repeated measures ANOVA, it had a significant main effect,  $F(1, 57) = 9.55, p = .003, \eta_p^2 = .14$ . A median split, shown in Fig. 4, revealed that individuals higher in worry had more positive (i.e., blunted) SPNs across all conditions than did those lower in worry. This result indicates that worry is associated blunting of anticipatory emotion.

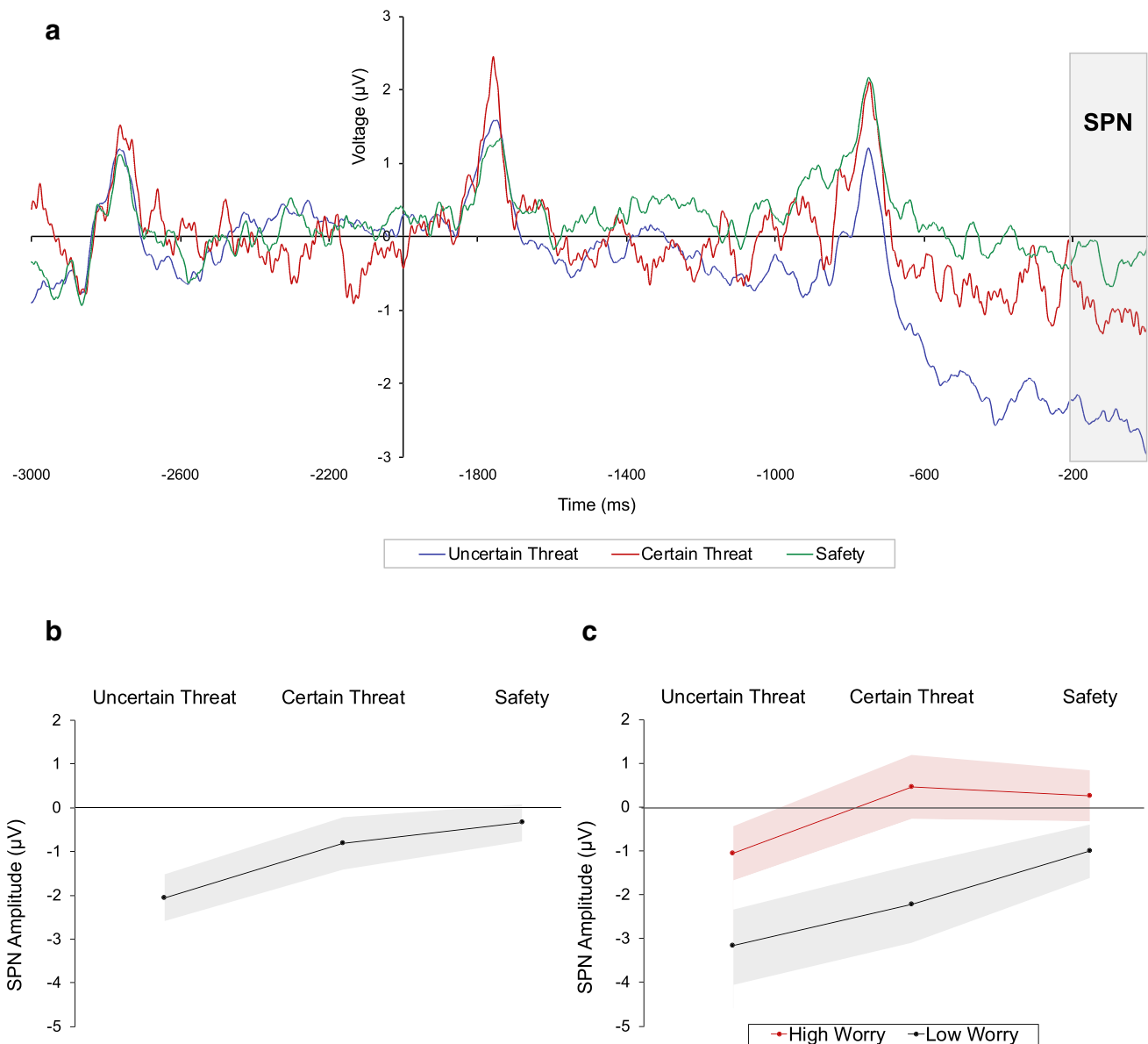
## Discussion

Uncertainty is part of everyday life. Although previous work has compared cognitive and emotional responding with certain versus uncertain outcomes, few studies have examined responses to varying levels of uncertainty. The current study investigated whether (1) attention and anticipatory emotion

are sensitive to small differences in the level of uncertainty, and (2) the effects of varying levels of uncertainty on attention and anticipatory emotion are moderated by individual differences in risk for anxiety disorders, specifically intolerance of uncertainty and worry. This study is the first to provide evidence for the sensitivity of early attention, measured by ERPs, to small variations in outcome uncertainty in the context of threat. Specifically, the P2 varied as a function of uncertainty—although in the opposite direction of what was hypothesized, with larger P2s elicited by stimuli denoting greater certainty. The result is consistent with literature showing that subtle differences in probability affect attention. For example, studies employing probability cueing paradigms have shown that early attention can track small differences in how frequently stimuli are presented in different spatial locations (Posner, 1980; Schwark & Dolgov, 2013). The current study extends this previous work, which was done outside of the context of threat, to show that early attention is sensitive to varying levels of outcome uncertainty in the context of threat. Given the result that early attention is affected by small differences in the degree of uncertainty, future work should consider employing designs that examine multiple levels of uncertainty in addition to comparing certain versus uncertain situations in order to more thoroughly investigate the effects of uncertainty on early attention.

Contrary to our hypotheses, in the current study, the P2 was smaller the more uncertainty was denoted by the stimulus. Based on previous studies examining the P2 in response to uncertainty and neuroimaging studies showing hypervigilance in clinically anxious populations (Dieterich et al., 2016; Grupe & Nitchke, 2013; Lin et al., 2015), we had hypothesized that uncertainty would lead to enhancement of the P2. However, there are differences between the current study and prior work that may account for the discrepant patterns of findings. Most notably, previous studies have only examined responding to uncertain versus certain events in a binary manner (Dieterich et al., 2016; Lin et al., 2015). In such designs, the difference between the uncertain and certain conditions is large (e.g., a 50% difference in probability), and the cue signaling uncertainty is thus highly informative. On the other hand, the current study employed a wide range of levels of uncertainty, which better represents the uncertainty encountered in daily life. Within the context of a wide range of levels of uncertainty, any specific probability is less informative about what the outcome will be. Relative differences in the informational value of cues may account for differences in attention. Indeed, theories of selective attention propose that uncertain stimuli are less informative than certain stimuli and thus warrant less attention (Esber & Haselgrove, 2011; Kruschke, 2001; Mackintosh, 1975). Thus, differences in the relative informational value between conditions could explain the different pattern of findings between the current study and prior work. As well, previous work (e.g.,

<sup>6</sup> The pattern of results across all of the analyses of the SPN is the same when the certain shock and certain safety cards are included.



**Fig. 4** Activity in the final 3,000 ms of the second anticipation period at Fz, F1, and F2. The SPN was calculated in the 200 ms preceding the outcome of the trial (i.e., the delivery or absence of a shock). Baseline correction was done using the interval of 1,000 to 2,000 ms following the revelation of the computer's card. a Mean amplitude of the SPN in the

second anticipation period for uncertain threat, certain threat, and safety. b A median split showing the effects of uncertainty on the SPN among those with high and low scores on the Penn State Worry Questionnaire. (Color figure online)

Dieterich et al., 2016; Lin et al., 2015) has focused on the P2 in response to cues that directly predict the probability of an aversive stimulus (e.g., signal a 50% probability if a negative picture). In the current study, cues predicted the probability of losing on a trial, which was associated with a 50% chance of shock. It is possible that differences in how proximal to and predictive of threat a cue is could affect how uncertainty impacts the P2 in response to the cue. Future work should systematically explore which factors, such as the range of uncertainty levels presented or the type of uncertainty (e.g., temporal versus outcome), may impact whether uncertainty enhances or diminishes early attention.

In addition, different theories of attention and learning make different predictions about the relation between uncertainty and attention. In line with a classic model that posits that attention is preferentially devoted to more uncertain cues (Pearce & Hall, 1980), we hypothesized that the P2 would be enhanced by uncertainty. However, a competing model states that uncertain stimuli are less informative than certain stimuli and thus warrant less attention (Mackintosh, 1975). More recent work has argued that principles of both models may be relevant in different situations (Pearce & Mackintosh, 2010). In the task used in the current study, no contingent behavior can be undertaken, and the association between the

stimulus and the outcome is explicit (i.e., a certain probability of shock)—in this context, little learning is necessary. It is possible that in circumstances where learning demands are low, uncertainty diminishes the attention paid to cues. Future work is necessary to explore whether the need for learning associations between stimuli and behavior influences the effects of uncertainty on attention.

Examining attention to varying levels of uncertainty may be particularly important in the context of understanding risk for anxiety disorders. Indeed, the quadratic effect of uncertainty on the P2 was greater among individuals who reported higher levels of IU. This finding suggests that IU is associated with greater differential deployment of attention based on the level of uncertainty denoted by a stimulus, with more certain stimuli eliciting more attention than uncertain stimuli. Previous work at the self-report and behavioral levels has shown that individuals higher in IU are more motivated than those lower in IU to reduce uncertainty in the environment (Buhr & Dugas, 2002; Luhmann, Ishida, & Hajcak, 2011; Tanovic, Hajcak, & Joormann, 2018a). More uncertain stimuli convey less information about what the outcome will be than do more certain stimuli and are thus less informative for reducing uncertainty. Deploying differing levels of attention based on how much uncertainty is conveyed by a stimulus may be a mechanism that enables higher IU individuals to preferentially attend to information that is more informative for reducing uncertainty. Importantly, the current results suggest that there is not one specific level of uncertainty that individuals at risk for anxiety disorders respond excessively to, in contrast to what has been suggested in previous literature (e.g., Carleton, 2012). Instead, individuals at risk for anxiety disorders discriminate more finely between varying levels of uncertainty than do those at lower risk.

Prospective and inhibitory IU appear to have differential relations with early attention to information about uncertain threat. In exploratory analyses, prospective IU was associated with larger P2 amplitude across all levels of uncertainty, while inhibitory IU was associated with a stronger quadratic effect of uncertainty on the P2. These data indicate that the two subscales, while related, may have different relationships with psychopathology and psychophysiological measures (for a review, see Tanovic, Gee, & Joormann, 2018b). It is possible that heightened early attention across all levels of uncertainty reflects the desire for predictability that is associated with prospective IU (Carleton, 2012). On the other hand, it is unclear why inhibitory IU, which is thought to reflect inhibition in the face of uncertainty, would be associated with greater differentiation between degrees of uncertainty denoted by a stimulus (Carleton, 2012). More work is needed to characterize the overlapping and distinct components of prospective and inhibitory IU, as well as their neural and psychophysiological correlates.

The SPN did not track specific levels of uncertainty but was instead largest for uncertain threat compared with certain threat and safety. Thus, anticipatory emotion may not be sensitive to small variations in uncertainty but may instead be influenced by whether a threatening stimulus is uncertain or certain broadly. The current study is the first to demonstrate that the SPN elicited immediately preceding an outcome is enhanced by uncertain threat. This finding extends previous literature on the SPN, which has found that it is enhanced by uncertainty (Catena et al., 2012; Foti & Hajcak, 2012; Seidel et al., 2015) and by threat (Böcker et al., 2001) independently. In light of the current findings, the SPN may be a useful tool to index anticipatory emotion in the face of uncertain threat that future studies should consider employing.

It is important to note, however, that the SPN may index a different aspect of anticipatory emotion than do SCRs and the startle reflex. Enhancement of the SPN by uncertain relative to certain threat parallels research demonstrating that SCRs and the startle reflex are enhanced by uncertainty in designs that do not vary the level of uncertainty (Davies & Craske, 2015; Grillon, 2008). However, previous work using similar tasks that varied level of uncertainty has reported that SCRs and the startle reflex are sensitive to variations in uncertainty (Chandrasekhar et al., 2008; Chin et al., 2016; Ring & Kaernbach, 2015). The startle reflex is thought to index defensive activation (Grillon, 2008), and SCRs are thought to index arousal irrespective of valence (Davis, 2006). One of the proposed generators of the SPN is the anterior insula, which has been hypothesized to play a key role in representing the anticipated emotional experience of a hypothetical future event (Grupe & Nitschke, 2013). It is possible that the SPN indexes the representation of anticipated future emotion when awaiting an uncertain stimulus and that this is distinct from the arousal and defensive activation indexed by SCR and the startle reflex (Davis, 2006; Grillon, 2008). Future work should employ multiple methods within the same design to examine convergence and divergence among different levels of analysis of anticipatory emotion.

The SPN across uncertain threat, certain threat, and safety was blunted among those who report a greater tendency to worry. This result is consistent with theory that suggests that worry is a mechanism by which emotion is avoided (Borkovec, Alcaine, & Behar, 2004). Greater blunting of the SPN in association with worry parallels findings examining the relation of psychophysiological indices of emotion with worry. For example, early work by Borkovec and Hu (1990) showed that individuals induced to worry about an anxiety-provoking situation exhibited lower heart rates than those instructed to think the situation neutrally. As well, the current results are consistent with work showing that the SPN in anticipation of both threatening and neutral images is blunted in those who report greater worry (Grant, Judah, White, & Mills, 2015).

The current study is limited by a few factors. First, the current sample did not consist of participants who meet diagnostic criteria for anxiety disorders. Instead, the goal was to examine how changes in the P2 and SPN in response to uncertainty relate to normal variation in traits associated with risk for the development of anxiety disorders. This is an important step for two reasons. First, by understanding how anticipatory responding to uncertainty is associated with traits that exist and vary in the general population, it is possible to begin to explore the mechanisms by which individual differences in responding to uncertainty may confer risk for the development of anxiety disorders. Second, our results suggest that future investigations utilizing clinical samples may be particularly informative if they focus on disorders like generalized anxiety disorder, which is characterized by high levels of both intolerance of uncertainty and worry (Freeston et al., 1994).

Another limitation of the current study is the cross-sectional nature of the design. Because participants were only examined at one time point, it is impossible to speculate as to whether variations in anticipatory responding to uncertainty result in risk for anxiety disorders or vice versa. Future research employing a longitudinal design is necessary to address this question. Similarly, the current study cannot conclude whether traits like IU and worry cause changes in attention and emotion in the face of uncertain threat. In addition to longitudinal research, studies employing an experimental design to manipulate IU and worry can address this question. For example, inducing worry and examining its effects on the SPN in response to uncertain threat would better disentangle whether worry blunts the SPN or whether a blunted SPN leads to worry.

It is important to note that the SPN across varying levels of uncertainty was examined immediately before participants learned whether they won or lost on a given trial. Although winning or losing had direct implications for whether participants would receive a shock and was only a few seconds removed from the shock delivery, it is possible that the threat was less salient in the first anticipation period than in the second. A difference in salience of the threat could contribute to differences in the magnitude of the SPN, which is influenced by attention and emotion (Brunia, van Boxtel, & Böcker, 2012). Future work should examine whether the SPN is sensitive to varying levels of uncertainty when a threatening stimulus is presented immediately following the anticipation period.

The current study, as well as previous work examining varying levels of uncertainty, focused on uncertainty regarding outcomes (e.g., whether or not a shock will be delivered) with known probabilities (e.g., a 50% chance of shock). However, other types of uncertainty exist in

daily life and can be manipulated in the laboratory—for example, temporal uncertainty (e.g., not knowing when a shock will be delivered) and intensity uncertainty (e.g., not knowing how intense a shock will be). The focus of the current study was on outcome uncertainty for three primary reasons. First, recent studies suggest that different forms of uncertainty may operate by common mechanisms to produce anxiety and elicit comparable levels of anxiety (Bennett, Dickmann, & Larson, 2018; Bradford, Shapiro, & Curtin, 2013; Hefner, Moberg, Hachiya, & Curtin, 2013). Second, outcome uncertainty lends itself most readily to manipulating varying levels. Uncertainty regarding timing, for example, can vary (e.g., a shock could be delivered sometime within 10 seconds of a cue or sometime within 20 seconds, with the latter being more uncertain), but outcome uncertainty provides a more straightforward opportunity to manipulate a wide range of levels. Third, outcome uncertainty is better suited than temporal uncertainty to examination with ERPs, which require precise and consistent timing across conditions. However, given the relevance of various types of uncertainty to everyday life, future work should examine the effects of varying degrees of multiple types of uncertainty on attention and emotion. By focusing on a single type of uncertainty, the current design avoided confounding the effects of multiple types as has been done in other commonly used tasks (e.g., the neutral-predictable-unpredictable [NPU] threat paradigm; Schmitz & Grillon, 2012) and provides the opportunity for future work to replicate findings across various types of uncertainty.

The current study provides evidence that both attention and emotion are important facets of anticipatory responding to uncertainty. Attention processes appear to track small changes in specific levels of uncertainty of a threat, while emotion processing is sensitive to whether a threat is uncertain broadly. Individuals higher in IU show greater differences in attention based on how much uncertainty is denoted by a stimulus, suggesting that they are more differentially sensitive to information regarding the uncertainty of threatening outcomes. Individuals who report worrying more show blunted emotion in the face of uncertain threat, consistent with the notion that worry serves as a way to avoid negative emotion. Altogether, these findings highlight the value of examining multiple aspects of anticipatory responding to varying levels of uncertainty for understanding risk for anxiety disorders.

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## References

- Barlow, D. H. (2004). *Anxiety and its disorders: The nature and treatment of anxiety and panic*. New York, NY: Guilford Press.
- Bennett, K. P., Dickmann, J. S., & Larson, C. L. (2018). If or when? Uncertainty's role in anxious anticipation. *Psychophysiology*, 55(7), e13066. doi:<https://doi.org/10.1111/psyp.13066>
- Böcker, K. B., Baas, J. M., Kenemans, J. L., & Verbaten, M. N. (2001). Stimulus-preceding negativity induced by fear: A manifestation of affective anticipation. *International Journal of Psychophysiology*, 43(1), 77–90.
- Borkovec, T. D., Alcaine, O. M., & Behar, E. (2004). Avoidance theory of worry and generalized anxiety disorder. In R. G. Heimberg, C. L. Turk, & D. S. Mennin (Eds.), *Generalized anxiety disorder: Advances in research and practice* (pp. 77–108). New York, NY: Guilford Press.
- Borkovec, T. D., & Hu, S. (1990). The effect of worry on cardiovascular response to phobic imagery. *Behaviour Research and Therapy*, 28(1), 69–73.
- Bradford, D. E., Shapiro, B. L., & Curtin, J. J. (2013). How bad could it be? Alcohol dampens stress responses to threat of uncertain intensity. *Psychological Science*, 24(12), 2541–2549.
- Brunia, C. H. M., van Boxtel, G. J. M., & Böcker, K. B. E. (2012). Negative slow waves as indices of anticipation: The Bereitschaftspotential, the contingent negative variation, and the stimulus-preceding negativity. In E. S. Kappenman & S. J. Luck (Eds.), *The Oxford handbook of event-related potential components* (pp. 1–22). Oxford, UK: Oxford University Press.
- Buhr, K., & Dugas, M. J. (2002). The Intolerance of Uncertainty Scale: Psychometric properties of the English version. *Behaviour Research and Therapy*, 40(8), 931–945.
- Carleton, R. N. (2012). The intolerance of uncertainty construct in the context of anxiety disorders: Theoretical and practical perspectives. *Expert Review of Neurotherapeutics*, 12(8), 937–947.
- Carleton, R. N., Norton, M. A. P. J., & Asmundson, G. J. G. (2007). Fearing the unknown: A short version of the Intolerance of Uncertainty Scale. *Journal of Anxiety Disorders*, 21(1), 105–117.
- Catena, A., Perales, J. C., Megías, A., Cándido, A., Jara, E., & Maldonado, A. (2012). The brain network of expectancy and uncertainty processing. *PLOS ONE*, 7(7), e40252.
- Chandrasekhar, P. V., Capra, C. M., Moore, S., Noussair, C., & Berns, G. S. (2008). Neurobiological regret and rejoice functions for aversive outcomes. *NeuroImage*, 39(3), 1472–1484.
- Chin, B., Nelson, B. D., Jackson, F., & Hajcak, G. (2016). Intolerance of uncertainty and startle potentiation in relation to different threat reinforcement rates. *International Journal of Psychophysiology*, 99, 79–84.
- Crouch, T. A., Lewis, J. A., Erickson, T. M., & Newman, M. G. (2017). Prospective investigation of the contrast avoidance model of generalized anxiety and worry. *Behavior Therapy*, 48(4), 544–556.
- Davies, C. D., & Craske, M. G. (2015). Psychophysiological responses to unpredictable threat: Effects of cue and temporal unpredictability. *Emotion*, 15(2), 195–200.
- Davis, M. (2006). Neural systems involved in fear and anxiety measured with fear-potentiated startle. *American Psychologist*, 61(8), 741–756.
- Dieterich, R., Endrass, T., & Kathmann, N. (2016). Uncertainty is associated with increased selective attention and sustained stimulus processing. *Cognitive, Affective, & Behavioral Neuroscience*, 16(3), 447–456.
- Dugas, M. J., Buhr, K., & Ladouceur, R. (2004). The role of intolerance of uncertainty in etiology and maintenance. In R. G. Heimberg, C. L. Turk, & D. S. Mennin (Eds.), *Generalized anxiety disorder: Advances in research and practice* (pp. 143–163). New York, NY: Guilford Press.
- Esber, G. R., & Haselgrove, M. (2011). Reconciling the influence of predictiveness and uncertainty on stimulus salience: A model of attention in associative learning. *Proceedings: Biological Sciences*, 278(1718), 2553–2561.
- Foti, D., & Hajcak, G. (2012). Genetic variation in dopamine moderates neural response during reward anticipation and delivery: Evidence from event-related potentials. *Psychophysiology*, 49(5), 617–626.
- Freeston, M. H., Rhéaume, J., Letarte, H., Dugas, M. J., & Ladouceur, R. (1994). Why do people worry? *Personality and Individual Differences*, 17(6), 791–802.
- Gorka, S. M., Lieberman, L., Shankman, S. A., Phan, K. L. (2017). Startle potentiation to uncertain threat as a psychophysiological indicator of fear-based psychopathology: An examination across multiple internalizing disorders. *Journal of Abnormal Psychology*, 126(1), 8–18.
- Grant, D. M., Judah, M. R., White, E. J., & Mills, A. C. (2015). Worry and discrimination of threat and safety cues: An event-related potential investigation. *Behavior Therapy*, 46(5), 652–660.
- Gratton, G., Coles, M. G., & Donchin, E. (1983). A new method for off-line removal of ocular artifact. *Electroencephalography and Clinical Neurophysiology*, 55(4), 468–484.
- Grillon, C. (2008). Models and mechanisms of anxiety: Evidence from startle studies. *Psychopharmacology*, 199(3), 421–437.
- Grupe, D. W., & Nitschke, J. B. (2013). Uncertainty and anticipation in anxiety: An integrated neurobiological and psychological perspective. *Nature Reviews Neuroscience*, 14(7), 488–501.
- Hajcak, G., Weinberg, A., MacNamara, A., & Foti, D. (2011). ERPs and the study of emotion. In E. Kappenman & S. Luck (Eds.), *The Oxford handbook of event-related potential components* (pp. 441–472). New York, NY: Oxford University Press.
- Hefner, K. R., & Curtin, J. J. (2012). Alcohol stress response dampening: Selective reduction of anxiety in the face of uncertain threat. *Journal of Psychopharmacology*, 26(2), 232–244.
- Hefner, K. R., Moberg, C. A., Hachiya, L. Y., & Curtin, J. J. (2013). Alcohol stress response dampening during imminent versus distal, uncertain threat. *Journal of Abnormal Psychology*, 122(3), 756–769.
- Koenig, S., Uengoer, M., & Lachnit, H. (2017). Attentional bias for uncertain cues of shock in human fear conditioning: Evidence for attentional learning theory. *Frontiers in Human Neuroscience*, 11, 266.
- Kruschke, J. K. (2001). Toward a unified model of attention in associative learning. *Journal of Mathematical Psychology*, 45(6), 812–863.
- Lin, H., Jin, H., Liang, J., Yin, R., Liu, T., & Wang, Y. (2015). Effects of uncertainty on ERPs to emotional pictures depend on emotional valence. *Frontiers in Psychology*, 6, 1927.
- Luck, S. J. (2014). *An introduction to the event-related potential technique* (2nd ed.). Cambridge, MA: MIT Press.
- Luhmann, C. C., Ishida, K., & Hajcak, G. (2011). Intolerance of uncertainty and decisions about delayed, probabilistic rewards. *Behavior Therapy*, 42(3), 378–386.
- Mackintosh, N. J. (1975). A theory of attention: Variations in the associability of stimuli with reinforcement. *Psychological Review*, 82(4), 276–298.
- McEvoy, P. M., & Mahoney, A. E. J. (2012). To be sure, to be sure: Intolerance of uncertainty mediates symptoms of various anxiety disorders and depression. *Behavior Therapy*, 43(3), 533–545.
- Meyer, T. J., Miller, M. L., Metzger, R. L., & Borkovec, T. D. (1990). Development and validation of the Penn State Worry Questionnaire. *Behaviour Research and Therapy*, 28(6), 487–495.
- Moser, J. S., Moran, T. P., Schroder, H. S., Donnellan, M. B., & Yeung, N. (2013). On the relationship between anxiety and error monitoring: A meta-analysis and conceptual framework. *Frontiers in Human Neuroscience*, 7, 466.
- Nelson, B. D., Hajcak, G., & Shankman, S. A. (2015). Event-related potentials to acoustic startle probes during the anticipation of

- predictable and unpredictable threat. *Psychophysiology*, 52(7), 887–894.
- Oglesby, M. E., Boffa, J. W., Short, N. A., Raines, A. M., & Schmidt, N. B. (2016). Intolerance of uncertainty as a predictor of post-traumatic stress symptoms following a traumatic event. *Journal of Anxiety Disorders*, 41, 82–87.
- Pearce, J. M., & Hall, G. (1980). A model for Pavlovian learning: Variations in the effectiveness of conditioned but not of unconditioned stimuli. *Psychological Review*, 87, 532–552.
- Pearce, J. M., & Mackintosh, N. J. (2010). Two theories of attention: A review and a possible integration. In C. Mitchell & M. E. LePelley (Eds.), *Attention and Learning* (pp. 11–39). New York, NY: Oxford University Press.
- Peters, A., McEwen, B. S., & Friston, K. (2017). Uncertainty and stress: Why it causes diseases and how it is mastered by the brain. *Progress in Neurobiology*, 156, 164–188.
- Posner, M. I. (1980). Orienting of attention. *Quarterly Journal of Experimental Psychology*, 32(1), 3–25.
- Ring, P., & Kaernbach, C. (2015). Sensitivity towards fear of electric shock in passive threat situations. *PLoS ONE*, 10(3), e0120989.
- Rossignol, M., Campanella, S., Bissot, C., & Philippot, P. (2013). Fear of negative evaluation and attentional bias for facial expressions: An event-related study. *Brain and Cognition*, 82(3), 344–352.
- Schmitz, A., Grillon, C. (2012). Assessing fear and anxiety in humans using the threat of predictable and unpredictable aversive events (the NPU-threat test). *Nature Protocols*, 7(3), 527–532.
- Schwark, J., & Dolgov, I. (2013). The influence of spatial and feature probability cuing in visual search. *Perception*, 42(4), 470–472.
- Seidel, E.-M., Pfabigan, D. M., Hahn, A., Sladky, R., Grahl, A., Paul, K., . . . Lamm, C. (2015). Uncertainty during pain anticipation: The adaptive value of preparatory processes. *Human Brain Mapping*, 36(2), 744–755.
- Skodzik, T., Zettler, T., Topper, M., Blechert, J., & Ehring, T. (2016). The effect of verbal and imagery-based worry versus distraction on the emotional response to a stressful in-vivo situation. *Journal of Behavior Therapy and Experimental Psychiatry*, 52, 51–58.
- Tanovic, E., Gee, D. G., & Joormann, J. (2018a). Intolerance of uncertainty: Neural and psychophysiological correlates of the perception of uncertainty as threatening. *Clinical Psychology Review*, 60, 87–99.
- Tanovic, E., Hajcak, G., & Joormann, J. (2018b). Hating waiting: Individual differences in willingness to wait in uncertainty. *Journal of Experimental Psychopathology*, 9(1), 1–12.
- Young, C. C., & Dietrich, M. S. (2015). Stressful life events, worry, and rumination predict depressive and anxiety symptoms in young adolescents. *Journal of Child and Adolescent Psychiatric Nursing*, 28(1), 35–42.