Psychophysiology, 39 (2002), 835–850. Cambridge University Press. Printed in the USA.

DOI: 10.1017/S0048577202010302

Affective modulation of eyeblink startle with reward and threat

ALEXANDER J. SKOLNICK[a] AND RICHARD J. DAVIDSON[a,b]
[a]Department of Psychology, University of Wisconsin, Madison, Wisconsin, USA
[b]Department of Psychiatry, University of Wisconsin, Madison, Wisconsin, USA

Abstract

An emotion-modulated acoustic startle paradigm for inducing positive and negative affect was used to address pregoal and postgoal affect. Participants played a computerized lottery task in which they chose digits that could match a subsequently displayed, random set of numbers. In the positive conditions, matches led to monetary rewards. In the negative condition, matches led to an aversive noise blast. In three experiments, we found eyeblink startle magnitude was potentiated just prior to feedback concerning reward outcome, suppressed following the feedback that a monetary reward was won, and potentiated when threatened with an aversive noise. When presented with a 0%, 45%, 90%, or 100% chance of winning, higher probabilities suppressed startle response after feedback whereas the 45% trials did not. These data indicate that postgoal positive affect (winning reward) reliably suppressed the startle response whereas pregoal positive affect did not.

Descriptors: Emotion-modulated startle, Reward, Threat, Positive affect, Anticipation

Affective modulation of startle eyeblink has become a standard measure with which to physiologically and objectively investigate emotional responses. The magnitude of the startle eyeblink response has repeatedly been shown to be sensitive to the valence of affective stimuli. People show increased blink magnitude when presented with negatively valenced or aversive stimuli and decreased blink magnitude when presented with positive or appetitive stimuli (Dawson, Schell, & Böhmelt, 1999; Lang, Bradley, & Cuthbert, 1990). This general pattern is found regardless of the sensory modality of the stimuli (Bradley, Cuthbert, & Lang, 1999). The enhancement of the startle response with negative stimuli is presumably due to matching the aversive motivational state induced by the negative stimuli with the negatively valenced defensive reflex (Lang, 1995; Lang et al. 1990). Conversely, the reduced startle response with positive stimuli appears to be the result of a mismatch between the appetitive motivational state induced by the positively valenced stimuli and the negatively valenced defensive reflex. The stimuli's degree of arousal level also interacts with the valence to affect the emotional modulation of startle. For example, Cuthbert, Bradley, and Lang (1996) found that the most arousing stimuli of either positive or negative valence showed the greatest modulation of the startle response.

Although the affective modulation of the startle response by negative-valenced stimuli is very robust, the effects of positively valenced stimuli are less robust, even though most studies match positive and negative stimuli for rated arousal levels. Most studies that found significant potentiation of the startle response to negatively valenced stimuli compared to either neutral or positively valenced stimuli found no significant effects comparing positive and neutral conditions using picture stimuli (Bradley, Cuthbert, & Lang, 1990, 1996; Larson, Ruffalo, Nietert, & Davidson, 2000; Vrana, Spence, & Lang, 1988), films (Jansen & Frijda, 1994), sounds (Bradley & Lang, 2000), odors (Ehrlichman, Brown, Zhu, & Warrenburg, 1995; Miltner, Matjak, Braun, Diekmann, & Brody, 1994), or imagery (Cook, Hawk, Davis, & Stevenson, 1991; Vrana, 1995). Suppression of the startle response to positive stimuli may be more dependent on the arousal level of the stimuli than the response to negative stimuli, as significant startle suppression is mostly seen with highly arousing erotic stimuli (Vrana et al., 1988, when only comparing erotic stimuli; Koukounas & Over, 2000 using erotic films; Manber, Allen, Burton, & Kaszniak, 2000, comparing erotic to action stimuli; Sabatinelli, Bradley & Lang, 2001, comparing erotic stimuli to objects). A few other studies have found significant startle inhibition to positive stimuli using pictures (Sutton, Davidson, Donzella, Irwin, & Dottl, 1997, presenting each valence separately; Codispoti, Bradley & Lang, 2001;

Alexander J. Skolnick was supported by an individual NRSA postdoctoral fellowship award (F32 MH11693). This work was also supported by NIMH Grants R01-MH40747, R37-MH43454, P50-MH52354 to RJD. Portions of this research were presented at the 1999 and 2000 annual meetings of the Society for Psychophysiological Research.

We thank Adrian Pederson for computer programming, Christine Larson for much helpful advice, and Jennifer Sontag and Michelle Mertz for assistance in data collection and analysis. We are grateful to Katherine Putnam, Carien Van Reekum, and Pam Tannenbaum for comments on earlier versions.

Address requests for reprints to: Richard J. Davidson, Laboratory for Affective Neuroscience, Department of Psychology, University of Wisconsin, 1202 W. Johnson St., Madison, WI 53706, USA. E-mail: rjdavids@facstaff.wisc.edu.

Putnam, Gooding, Larson, Jackson, & Davidson, 1999, presenting affective pictures for only 500 ms) and odor in a between-subjects design (Ehrlichman, Brown Kuhl, Zhu, & Warrenburg, 1997).

The lack of strong effects of positive affect on the startle response may be due to the nature of the tasks used. By having subjects passively view or listen to stimuli to elicit positive affective states, positive affect may be elicited without a strong approach component. It may be the case that to generate sufficient changes in the activation of neural circuitry involved in approach/appetitive processes assumed to underlie positive affect (Davidson & Irwin, 1999), subjects must be more engaged with the task such that they can actively obtain positively valenced stimuli (such as a desirable reward) instead of passively experiencing positive stimuli. Reward processes influence adaptive behavior leading to successful survival and reproduction and are integral to approach systems. Rewarding stimuli are more likely to invoke approach systems than stimuli either not tied to reward or stimuli tied to punishment. Thus, active task engagement that has the prospect of reward may have a more potent effect of inducing approach-related positive affect than a passive viewing condition.

The appetitive and consummatory components of an organism attaining a reward likely have different ramifications for positive affect processes. Davidson (1994, 1998) has suggested that while seeking out and obtaining a reward, approach-related positive affect is likely to occur (pregoal attainment positive affect). Positive affect related to the consummatory response after obtaining a reward, however, is unlikely to activate approach processes, but represents something akin to contentment (postgoal attainment positive affect). There are likely important neurobiological differences between pregoal and postgoal attainment positive affect related to the role of prefrontal cortex and other subcortical structures such as the ventral striatum and nucleus accumbens (Davidson, 1998; Davidson & Irwin, 1999). Recently, Knutson, Fong, Adams, Varner, and Hommer (2001), using event-related functional imaging, found differences in pregoal and postgoal positive affect in a reward paradigm. Anticipation of reward activated ventral striatum, whereas rewarded outcomes activated ventromedial frontal cortex. Interestingly, the data on the neural substrates of startle suppression to reward implicate these circuitries, especially those involving the nucleus accumbens. Koch, Schmid, and Schnitzler (1996) lesioned either the nucleus accumbens or the amygdala prior to conditioning a light with desirable food. Only lesions of the nucleus accumbens blocked the attenuation of the startle response found in controls and amygdala-lesioned animals. Dopamine from the nucleus accumbens likely plays an important role in sensorimotor integrations that facilitate pregoal approach behavior (Ikemoto & Panksepp, 1999) and modulate startle circuitry.

Research with both humans and nonhuman animals have shown diminution of startle in a nonaversive conditioning paradigm. Two studies (Hamm & Vaitl, 1996; Lipp, Sheridan, & Siddle, 1994) used a rewarded reaction time design in which the rewarded conditioned stimulus (CS+) signaled a trial with the chance to win money with a quick response. Both studies found reduced startle magnitude during CS+ trials signaling potential reward as compared to trials when CS+ signaled shock. However, neither study found startle magnitude during CS+ signaling reward to be significantly inhibited as compared with control trials. Two studies with rats have shown that appetitive rewarding stimuli can suppress the startle response compared to controls. When food-deprived rats were conditioned to a light-signaled reward (desirable food and water), startle amplitude was suppressed compared to unconditioned controls (Koch et al., 1996; Schmid, Koch, & Schnitzler, 1995).

A few preliminary studies examined startle responsiveness during anticipation of a positive versus negative outcome. Two studies looked at startle modulation during anticipation of upcoming affective slides after a warning signal (Allen, Wong, Kim, & Trinder, 1996; Erickson, Levenston, Curtin, Goff, & Patrick, 1995) and one examined startle responses during a warning period prior to a reaction time task and after receiving feedback concerning a win or loss (Spence & Cook, 1993). Although these reports were not detailed, they did find affective modulation of startle (decreased magnitude) during anticipation (pregoal) of positive slides and the chance to win money but not during postgoal attainment positive affect (after receiving reward feedback; Spence & Cook, 1993). More recent reports have also used cueing of the valence of upcoming affective slides to examine the anticipation of positive stimuli (Nitschke et al., 2002; Sabatinelli et al., 2001). Both studies found that anticipation of both positive (and negative) stimuli produced *larger* startle responses than anticipation of neutral stimuli, although Nitschke et al. found anticipation of positive stimuli significantly reduced startle magnitude compared to anticipation of negative stimuli. However, reservations are warranted in the interpretation of the latter two studies. In Nitschke et al., the difference between anticipatory startle between neutral and positive was only marginally significant, and Sabatinelli et al. only used male subjects scoring high in fear of snakes, so the validity to non-high-fear subjects remains in question.

During periods of anticipation, it is possible that modality of the stimuli and direction of attentional focus modulate startle responsiveness as in the above studies. Directing attentional resources to stimuli leaves fewer resources that can be directed to the startle probe. Thus, when attention is directed away from the startle probe itself (e.g., to a warning stimulus), a diminution of startle magnitude is usually seen (Hackley, 1999). This issue is further complicated by the fact that studies using different paradigms have found different effects of attentional deployment on startle responsiveness: inhibition (Hackley, 1999; Putnam & Vanman, 1999), facilitation (Jennings, Schell, Filion, & Dawson, 1996; Lipp, Siddle & Dall, 1997, 1998, 2000), or little or no effect (Cuthbert, Schupp, Bradley, McManis, & Lang, 1998; Vanman, Boehmelt, Dawson, & Schell, 1996).

Across the studies that have investigated startle responses to positively valenced stimuli, there is variability in the manner that positive affect was addressed. Whereas some studies probed subjects during a pregoal phase (e.g., Hamm & Vaitl, 1996; Lipp et al., 1994; Nitschke et al., 2002; Sabatinelli et al., 2001; Schmid et al. 1995) most studies have probed emotional states during a phase akin to a postgoal phase in which subjects passively experienced positive stimuli. Given this variability, the origin of the effects of positive affect remains unclear and requires systematic examination. We created the current paradigm to enable us to separately examine these two components (pregoal and postgoal positive affect) in a within-subject design.

The following "lottery paradigm" was used to induce both positive and negative affect without the use of pictorial stimuli, loosely based on a experimental design of Grillon et al. (Grillon, Ameli, Merikangas, Woods, & Davis, 1993; Grillon, Ameli, Woods, Merikangas, & Davis, 1991). In Grillon's studies, subjects were given cues that they should either anticipate a possible negative event (e.g., electric shock) or not and startle responses were measured while the subjects waited for each trial's outcome. In the present paradigm, participants performed an engaging computerized lottery task in which they chose digits that could or could not match with another randomly displayed set of digits. They entered their numbers, watched the numbers "spin" for 10 s, and then received feedback as to whether they had a lottery match or not. Trials were designed such that acoustic startle probes were presented either before or after receiving visual feedback in both positive and negative conditions.

In Experiment 1, we ran both positive (reward) and negative (threat) conditions. The reward and threat conditions paralleled each other in structure. In the positive condition, on each trial, participants knew whether they had a chance to win a monetary reward or not. There was no punishment condition; participants never lost money. In each trial of the negative condition, participants knew whether they had a chance to receive a loud aversive noise or no chance to receive the noise. Startle probes were presented either early or late in the anticipatory (or prefeedback) period, and soon after they received feedback and in the middle of a blank-screen intertrial interval. Experiments 2 and 3 addressed how participants responded to the anticipation of reward. In these experiments participants were presented with three different probabilities of receiving a reward and how these different expectancies affected their startle responses was measured. Independent samples were tested in each study to assess the replicability of the basic effects.

EXPERIMENT 1

The lottery paradigm allowed us to test several hypotheses concerning startle responsiveness to situations invoking positive or negative affect. When presenting participants with trials in which they had a chance to win money, we could test whether pregoal, postgoal, or both types of positive affect suppressed the startle. During the prefeedback period, while participants waited to find out if they won, we hypothesized that the expectation of reward (pregoal positive affect) would suppress startle eyeblink magnitude. Specifically, we predicted that prefeedback startle eyeblink magnitude would be smaller during trials in which there was a chance to win than when there was no chance to win. This hypothesis followed from the theory that pregoal positive affect most likely activates approach processes and from research on signaling of reward in rats and humans (Lipp et al., 1994; Schmid et al., 1995). An alternative prediction would suggest an increase in startle magnitude during a pregoal period due to differing task demands (Lipp et al., 1997, 1998, 2000) instantiated by the different chances to win money. Knowing there is a chance to win could increase the attention paid to the spinning numbers as compared to trials when there was no chance to win. If receiving feedback about a positive reward outcome is a pleasant experience, then we also expected to find suppression of the startle response postfeedback. Specifically, rewarded trials should produce smaller blinks than nonrewarded trials or trials in which there was no chance to receive a reward. Although receiving a reward is not expected to involve approach processes, it should generate positive affect, which would likely cause a mismatch with the defensive startle reflex, reducing startle amplitude. No effects due to task demand in this period were expected when comparing rewarded to nonrewarded trials, as the only difference between conditions was the type of feedback.

The negative version was used to replicate the fear-potentiated startle paradigm in humans (Grillon et al., 1991, 1993) using the threat of noise during anticipation of a negative event. In contrast to the reward condition, we anticipated that the startle responses would be potentiated at the probe immediately prior to receiving feedback and at the probe presented after receiving feedback that the aversive noise will be delivered. The positive and negative conditions were identical in structure except for the outcome.

Experiment 1 was divided into a portion where subjects performed all the reward or threat conditions in one block without a break (1a) and a portion where reward and threat trials were each divided into three blocks of trials (1b). The change to dividing sessions into blocks was made to present winnings more frequently than only at the end of all the trials. No major differences were expected or found between these two versions, therefore they were combined for statistical analyses.

Methods

Participants

Sixteen women and 6 men participated in the Experiment 1a and 12 women and 7 men participated in Experiment 1b (aged 18–28 years). Participants were recruited by advertisement and word of mouth. Incentive for participation was the knowledge that money would be won in the experiment. All participants were told, "Most participants win more than $10." Payment for participation was the money "won" (fixed at $52). Five participants were dropped due to an insufficient number of startle responses, leaving a total sample of 36 (mean age = 20.9), once the two experiments were combined.

General Procedure

Participants were given an overview of the experiment and asked to sign a consent form. They sat comfortably, while wearing headphones, in front of a 17-in. NEC-6FG multi-sync monitor on which all stimuli were displayed. Three electrodes for recording EMG responses were applied to the face before participants received detailed instructions for the task. They were told that the study examined facial responsiveness during the lottery task. Emotional aspects were never mentioned.

Participants were given two or three practice trials for each part of the experiment to explain the task. At the start of the experiment, participants viewed a blank screen and received nine startle probes spaced apart by 18–22 s in order to habituate the early large startle responses. The order of blocks of experimental trials following the habituation trials was counterbalanced. At the conclusion, participants filled out questionnaires and were debriefed.

Experiment 1a: Reward Trials

Participants were told that for each trial they would enter six digits and try to match this set to another six-digit number. Any matches resulted in monetary gain. Participants were presented with a screen on which to enter a six-digit number. On the screen read, "Enter Your Lucky Number Here" and below were two sets of six dashes where the numbers entered appeared. Entering the sixth digit marked the beginning of each trial. Upon entering the sixth digit, the top row of digits remained while the bottom row began to rapidly change digits giving the appearance of spinning. This anticipatory period lasted 10 s, over which time the digits spun randomly, initially changing 20 times/s, and gradually slowed down to 3 times/s before stopping to display a new set of numbers. Immediately following the anticipatory period was a 3-s feedback period when the participant was informed as to whether they matched a digit(s) or not between their original selection (remaining on top) and the new display (at the bottom). Matched digits flashed in red; the amount of money won was displayed in red in the center of the screen along with a total of winnings thus far. A 6-s intertrial interval (ITI) consisting of a blank screen followed the feedback period after which a new trial was presented.

Trials were divided into reward trials in which the participants knew they could win money and neutral trials in which they knew they could not. Participants were alerted to the different trials by a message between the two rows of dashes: "chance of money" trial for reward trials and "no chance of money" trial for neutral trials. In a chance of money trial, any match resulted in monetary gain (matching one digit = \$0.50; two digits = \$1; three digits = \$2; four digits = \$5; five digits = \$20; six digits = \$50). During neutral trials, participants could either match or not match their set of digits, but the message during the feedback period read "No Money This Trial" regardless of the outcome. All participants experienced the same schedule of matches and nonmatches in a fixed sequence. Participants matched on half of both the 51 chance of money trials and 28 no chance of money trials (total = 79 trials). A quasi-random order of trials was generated such that each participant "won" \$52.00. Of the chance of money trials, participants received 25 nonmatching trials, 12 trials matching one digit, 6 trials matching two digits, 5 trials matching three digits, 2 trials matching four digits, and 1 trial matching five digits. Participants never matched six digits, and all money was distributed at the end of the experiment.

Startle probes were presented at either 2 s or 9 s after the trial began (anticipatory probes), 1.5 s after receiving the results (feedback probe), or 6 s after receiving results (ITI probe, 3 s into the ITI period) in a counterbalanced order (Figure 1). At each of the anticipatory probe times (2 s, 9 s), participants received seven startle probes for neutral trials and four probes for each of the matching and nonmatching reward trials. The anticipatory startle probes were collapsed between matching and nonmatching trials, as participants could not tell the outcome of these trials prior to the feedback period (for a total of eight probes each). For both the feedback and ITI probe times, a total of seven startle probes were administered for each condition (neutral, reward, no reward). Of the 79 trials, 7 trials were not probed.

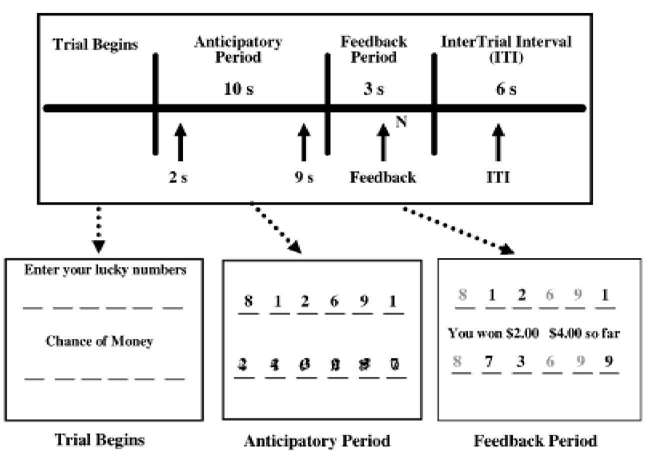

Figure 1. Design of the study. The top portion of the figure depicts a single trial that begins with a participant entering his or her six digits ("Trial Begins"). During the anticipatory period, the numbers on the lower part of the screen "spin." During the feedback period, the outcome of the trial is displayed. The bottom portion of the figure provides an example trial in which three digits matched (gray). For display purposes, the figure is shown in inverted colors compared with actual testing. Normally, the background was black, the letters and figures were white, and the feedback messages and matched digits were red. ↑ = probe presented. **N** = noise delivered: aversive noise in Experiment 1, positive noise (cheering) in Experiments 2 and 3.

Experiment 1b: Reward Trials

This procedure was identical to that of Experiment 1a except the reward block of trials was divided roughly equally into three parts such that there was a break after each third of the trials. At each break, participants were given the money they had won during the preceding block and they continued with the next block. Also, the feedback probe was delivered at 2 s instead of 1.5 s.

During this version of the experiment, the amount of time it took for each subject to enter each set of six digits for all reward and threat trials was recorded. Entering the first digit started the timer and it ended when the sixth digit was entered.

Experiment 1a: Threat Trials

Threat trials were identical to the reward trials in that participants had to enter a six-digit number each trial, each period was the same, as was the timing of the probes. Threat trials were divided into trials in which the participants knew there was a possibility of receiving a loud aversive noise blast and safe trials in which they knew there was no possibility of receiving the noise. Participants were alerted to the different trials by a message between the two rows of dashes: "Chance of Noise" trial for threat trials and "No Chance of Noise" trial for safe trials. Participants were informed that on a chance of noise trial, if they matched three digits or more they would receive the aversive noise through their headphones. The number of trials receiving the aversive noise was smaller than the number of rewarded trials to reduce possible habituation to the aversiveness of the noise. Participants were told that the more digits they matched the "larger the noise got." Matching three digits resulted in a 2-s noise, four digits resulted in a 3-s version of the noise, and five digits resulted in a 4-s version of the noise. During the feedback period, the display indicated any matched digits and whether they would receive the noise (message on screen: NOISE !) or not (message on screen: No Noise This Trial). If a noise was delivered, it occurred 2 s into the 3-s feedback period and played into the ITI. If the feedback probe was also presented, it always preceded the noise. The noise was delivered a total of eight times, the same number of times participants matched three, four, or five digits during the reward trials. Participants received a similar proportion of matches and nonmatches as in the reward trials (33% for reward; 37% for threat).

Startle probes were presented at the exact same times as in the reward trials (2, 9 s, feedback probe, or ITI probe) in a counterbalanced order. During the safe trials and threat trials in which no aversive noise was received, a total of seven startle probes were delivered during each of the four probe times. Trials in which participants received the aversive noise were only probed during the feedback and ITI periods due to the small number (eight) of trials with the aversive noise. Thus, there were four startle probes for each of the feedback and ITI probes on threat trials with the noise. Also, because no probes were delivered during the anticipatory period on threat trials when participants would match enough digits to receive the noise, no conditions were collapsed as in the reward analysis. Of the 68 threat trials, 4 trials were not probed.

Experiment 1b: Threat Trials

This procedure was identical to that of Experiment 1a except the threat block of trials was divided roughly equally into three parts such that there was a break after each third of the trials. Also, the feedback probe was delivered at 2 s and the noise, if delivered, occurred at 2.5 s.

Apparatus

Presentation of stimuli and acoustic startle probes were controlled by in-house software on a 100-MHz Pentium PC. The acoustic startle probe was a white noise burst 40 ms in duration, 95 dB, and with a nearly instantaneous rise time. Startle probes were generated with a Coulbourn S81-02 noise generator and a Coulbourn S82-24 audio-mixer power amplifier, and were delivered binaurally through Audio-Technica ATH-M3X headphones. The aversive noise was created by overlaying a smoke alarm, ringing bell, foghorn, and guitar electric feedback using Cool Edit Pro (Syntrillium Software Corporation, Phoenix, AZ) software. The sounds were from commercially available sound effects compact discs. The noise was played as a .WAV file lasting 2, 3, or 4 s, 97–98 dB, with a nearly instantaneous rise time.

Data Acquisition and Reduction

Raw and integrated EMG from the orbicularis oculi were collected (in microvolts) using two Sensormedics mini-electrodes placed directly below the left eye (as done by van Boxtel, Boelhouwer, & Bos, 1998). A third electrode was placed in the center of the forehead as a ground. The impedance for the electrode pair was less than 20 kΩ. Using SAI Bioelectric amplifiers (James Long Co., Caroga Lake, NY), EMG signals were filtered with a bandpass of 1–800 Hz and then amplified 10,000 times. After passing through a Rockland high pass filter set at 30 Hz, raw EMG signals were integrated and rectified using a Coulbourn S76-01 contour-following integrator with the time constant set at 20 ms. All signals were digitized at 500 Hz and stored on a 100 MHz Pentium PC throughout the stimuli presentation using SnapStream software (HEM Data Corporation, Springfield, MI) and a 12-bit analog-to-digital board (Analogic Corporation, Wakefield, MA). Recording equipment was calibrated before and after each session.

Orbicularis oculi EMG in response to acoustic startle probes was reduced to eyeblink reflex magnitudes using the following procedure. First, automatic peak and blink onset detection was performed on the integrated EMG response to each probe using in-house programming (using MATLAB, The MathWorks, Natick, MA). The authors then reviewed each response. Approximately 8% of eyeblink reflexes were excluded from further analyses due to excessive noise during a 50-ms, prestartle baseline period (e.g., blinks, unusually high amounts of integrated EMG during baseline) or because the onset of the integrated EMG eyeblink reflex began less than 20 ms following the startle probe. Eyeblink reflex magnitudes were calculated by subtracting the amount of integrated EMG at reflex onset from the peak amplitude (maximum amount of integrated EMG between 20 and 120 ms following probe onset). Trials with no perceptible eyeblink reflex were assigned a magnitude of zero and included in analysis. Finally, eyeblink reflex magnitudes were z-transformed within subjects due to large individual differences in the distribution of this measure and within block due to habituation over the course of the experiment. Blinks that were greater than three standard deviations above the mean for a given participant were excluded. There had to be at least three good blinks per participant per condition per probe time to be included in the analyses.

Data Analysis

All ANOVAs were repeated measures unless stated otherwise. Probe time (2 s, 9 s, feedback, ITI) and condition (reward, neutral, threat, safe) were always within-subject factors. Separate ANOVAs were performed on pre- and postfeedback probe times. This was necessary in the reward condition because collapsing matching and nonmatching trials in the prefeedback period made it incomparable to the postfeedback period where no collapsing across conditions occurred. Separate ANOVAS were also necessary for the threat condition due to the lack of probes during the prefeedback period when participants would receive the aversive noise. All ANOVAs using a within-subjects factor used a Huynh–Feldt correction where appropriate (Huynh & Feldt, 1970).

To test hypotheses that the startle blink will be affected by either expecting or receiving a monetary reward, separate repeated measures ANOVAs were used for the anticipatory period, feedback, and ITI probe times. Comparisons among reward, nonreward, and neutral trials were performed for each analysis on postfeedback probe times. Similarly, threat trials were analyzed separately for the anticipatory period, feedback, and ITI probe times. The possibility of order effects due to whether participants received reward or threat trials first was checked using ANOVAs with order as a between-group factor. Fluctuations in the degrees of freedom for the error term occurred because it was affected by missing cells that were dropped due to not having at least three good blinks for analyses.

To test for differences in startle responses between Experiments 1a and 1b, the two experiments were compared using repeated measures ANOVAs on blink magnitude, with probe time and condition as the repeated measures factors and experiment (1a, 1b) as the between-groups factor. An ANOVA comparing reward trials in Experiments 1a and 1b found no significant differences due to the main effect of experiment, or to any two-way or three-way interaction effects (all pertinent ps $> .15$). In an ANOVA comparing prefeedback threat trials, although the main effect for experiment was not significant, $F < 1.0$, the Probe Time × Experiment and Probe Time × Condition × Experiment interactions were significant, $F(1,30) = 5.65$, $p = .02$; $F(1,30) = 7.21$, $p = .01$, respectively. These significant interaction effects were due to differences in blink magnitude for safe trials during both anticipatory probe times: At the 2-s probe time, blinks were significantly smaller in safe trials of Experiment 1b than Experiment 1a, and at the 9-s probe time, blinks were significantly smaller in safe trials of Experiment 1a than Experiment 1b. Finally, in an ANOVA comparing postfeedback threat trials, no significant main effects or interactions were found (all pertinent ps $> .21$). Given that there were no significant differences in the reward trials or postfeedback threat trials between the two versions of Experiment 1, with only minor and inconsistent differences during some of the safe trials, the two experimental versions were combined for further analyses.

Results

Order Effects

The order in which the blocks of reward or threat trials were presented to participants significantly influenced the outcome for both reward and neutral trials in a straightforward fashion; blink magnitude was significantly larger when reward and neutral trials were presented prior to threat trials than when after (prefeedback probes, $F(1,28) = 33.82$, $p < .0001$; postfeedback probes, $F(1,28) = 7.36$, $p = .011$). There was no significant Order × Probe Time interaction in either case. When threat and safe trials were pre-

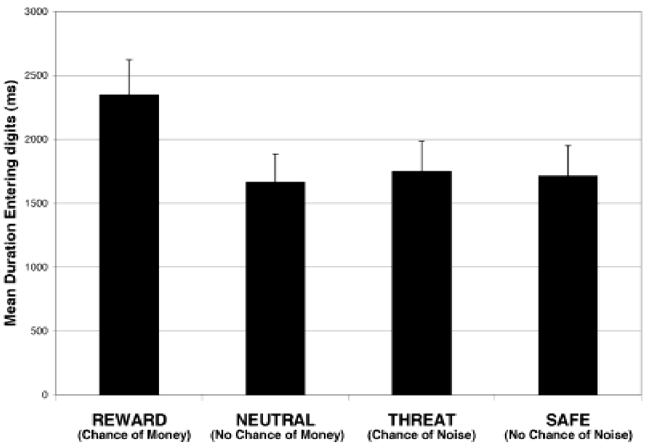

Figure 2. Mean duration (in milliseconds) to enter digits in Experiment 1 collapsed across blocks ($n = 15$). Error bars represent ± standard error of the mean.

sented prior to reward trials, there were no significant order effects for threat trials and no significant Order × Probe Time interaction. For safe trials, no main effect for order was found but the Order × Probe Time interaction was significant, $F(3,54) = 4.04$, $p = .012$. This effect was generated at the 2-s probe time where blink responses to safe trials were smaller when threat trials were presented prior to reward trials rather than the reverse. These order effects suggest habituation may be a factor overall, but does not affect the integrity of any effects at any one probe time.

Manipulation Check

To assess whether participants adjusted their behavior based on the trial type, the amount of time spent entering digits for each trial was examined (from Experiment 1b only, $n = 15$). The amount of time to enter digits for chance of money trials, no chance of money trials, chance of noise trials, and no chance of noise trials was compared (Figure 2). Trial type influenced how much time participants spent entering digits, $F(3,42) = 5.98$, $p = .005$, with participants spending the most time selecting digits on chance of money trials (compared to no chance of money trials, $p = .0024$). The threat of noise did not significantly affect the time taken to select digits (ps $> .5$).

Reward Trials[1]

Participants did not know the outcome of a chance of money trial until the feedback period. Therefore, no differences between the matching and nonmatching reward trials during the anticipatory period were expected. Paired t tests on the z-transformed data confirmed that reward outcome had no effect prior to feedback at both 2-s and 9-s probe times, $t(31) = 1.57$, n.s., $t(30) = 1.58$, n.s., respectively. Therefore, startle probes were collapsed (averaged) across reward and nonreward trials for the 2-s and 9-s probe times.

A Condition (chance of money, no chance of money trials) × Prefeedback Probe Time (2 s, 9 s) ANOVA found significant effects for both condition, $F(1,29) = 8.81$, $p = .006$, and probe time, $F(1,29) = 48.3$, $p = .0001$, and a marginally significant Condition × Probe Time interaction, $F(1,29) = 3.59$, $p = .068$. Pairwise comparisons showed that the combined reward blink magnitude at the 9-s probe time was significantly larger than the blink magnitude for the neutral trials, $p = .004$, as well as the 2-s responses, ps $< .0001$ (Figure 3). The magnitude of the blink response during neutral trials at the 9-s probe time was significantly larger than the neutral trials at 2 s, $p = .0014$.

In the postfeedback period, receiving a monetary reward affected the size of the startle response. An ANOVA comparing across conditions for the feedback startle probe found a marginally significant difference in blink magnitude, $F(2,58) = 3.09$, $p = .053$. Blink magnitude during matching trials was significantly smaller than during nonmatching trials, $p = .024$ (Figure 3). However, the feedback blink response during reward trials was not significantly smaller than neutral trials. Although the pattern of startle blinks at the ITI probe time was similar to the feedback probe, blink responses did not differ based on reward outcome, $F(2,64) = 1.46$, $p > .05$. The size of the reward ($0.50 to $20.00) had no significant effect on blink magnitude, ps $> .15$.

Threat Trials[2]

The anticipation of a possible threat (aversive noise) was hypothesized to potentiate the startle blink response. A Condition (threat, safe trials) × Probe Time (2 s, 9 s) ANOVA for probes administered during the anticipatory period supported this hypothesis by finding significant effects for condition, $F(1,31) = 9.51$, $p = .0043$, probe time, $F(1,31) = 39.37$, $p < .0001$, and the interaction between the two factors, $F(1,31) = 19.46$, $p < .0001$ (Figure 4). Pairwise contrasts confirmed that during threat trials, startle blink magnitude was increased at the 9-s probe compared to safe trials at 9 s, $p < .0001$, and compared to the 2-s probe, $p < .0001$. There was no affect of condition at the 2-s probe time.

During the feedback period, participants were presented a startle probe 500 ms prior to the onset of the noise. ANOVAs for both the feedback and ITI probe times confirmed the robust differences evident in Figure 4. Significant differences were found among the three conditions for the feedback probe, $F(2,62) = 60.05$, $p < .0001$. Importantly, startle blink responses were more potentiated during trials when participants were about to receive the noise than when participants learned at feedback that they would not receive noise (no-noise trials, $p = .0001$) or knew prior that they had no chance to receive the noise (safe trials, $p = .0001$). Also, a paired t test comparing threat trials at the 9-s probe and at feedback probe for trials when they received the noise confirms that the magnitude at the feedback probe was greater than at the 9-s probe, $t(32) = 4.54$, $p = .0001$. During the ITI, blink magnitude was also differentiated by noise and no-noise trials, $F(2,58) = 17.91$, $p < .0001$, but in the opposite direction. Trials in which subjects received the aversive noise showed significantly smaller

[1]Analyses of the raw untransformed data (A-D units) showed the same general effects and trends. At the prefeedback probe times, startle magnitude was significantly larger at 9 s than 2 s, regardless of condition, all ps $< .01$. At the 9-s probe, chance of money trials were significantly larger than no chance of money trials, $p = .01$. At the feedback probe, matching trials showed the same trend of being smaller than nonmatching trials, but it was not significant, $p = .31$. At the ITI probe, matching trials produced significantly smaller blinks than nonmatching, $p = .023$, or neutral trials, $p = .057$.

[2]Analyses of the raw data showed the same general effects. There was no condition difference at the 2-s probe time. At the 9-s probe, the chance of noise trials produced significantly larger blink responses than 9-s safe trials, $p = .011$. At the feedback probe, matching trials leading to the aversive noise potentiated the startle response to a greater extent than the no-noise and safe trials, both ps $< .0001$. At the ITI probe, blink magnitude was significantly smaller for trials when they received the noise compared to the other conditions (no-noise trials: $p = .004$; safe trials: $p = .005$).

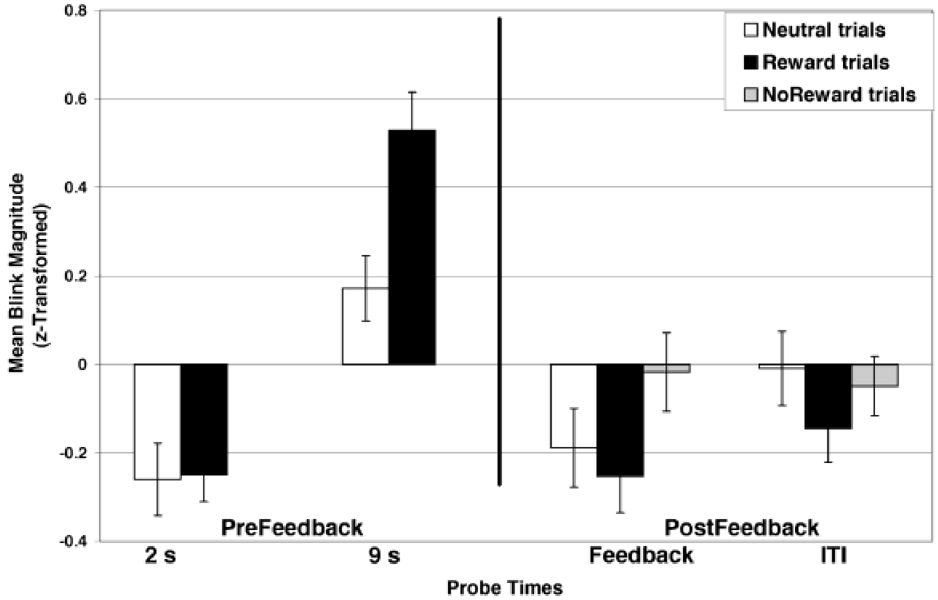

Figure 3. Standardized (*z* score) eyeblink magnitude averaged for each probe time for each reward condition in Experiment 1. Error bars represent ± standard error of the mean.

blink magnitudes as compared to either no-noise trials, $p = .0001$, or safe trials, $p = .0001$.

Discussion

These data do not support the hypothesis that the anticipation of a potential reward would suppress the startle eyeblink in humans compared to anticipation of no reward. On the contrary, we found the startle response was significantly potentiated compared to trials when subjects knew they could not win. The size of the mean response at the 9-s probe time was almost equivalent to the same response during the threat conditions when subjects were possibly expecting an outcome of an aversive noise. One possible explanation for finding larger startle responses to anticipation of a potential reward may be that the conditions of the study inadvertently generated negative affect. Participants spent significantly more

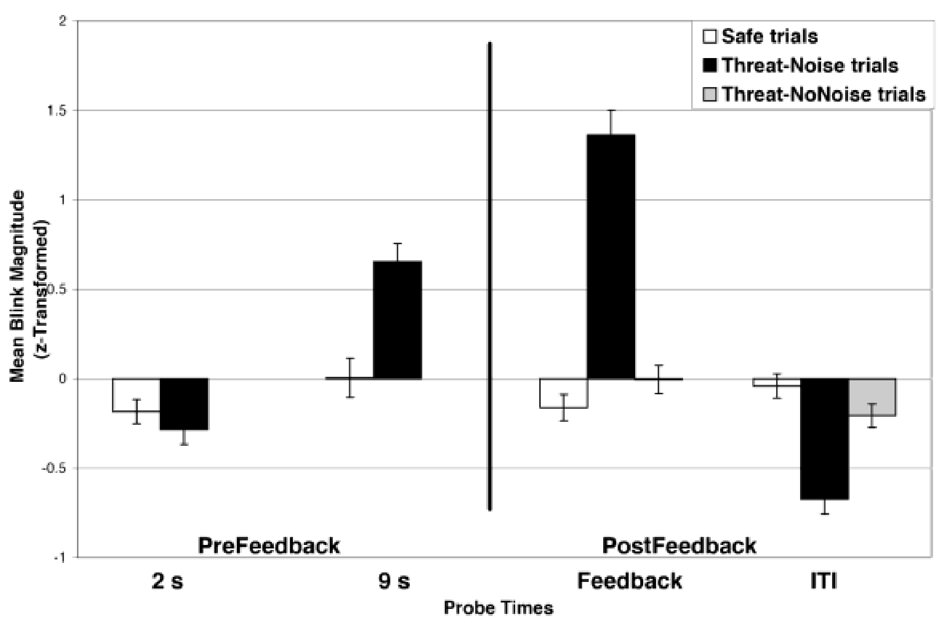

Figure 4. Standardized (*z* score) eyeblink magnitude averaged for each probe time for each threat condition in Experiment 1. Error bars represent ± standard error of the mean.

time entering their numbers when there was a chance of winning money, suggesting that they may have been invested in the outcome of those trials. They always had the chance of winning a relatively large reward ($20 or $50). Combined with the uncertainty of obtaining a matching set of digits, we may have created an anxiogenic situation facilitating the startle response (*sensu* Grillon et al., 1991). This explanation will be examined in Experiments 2 and 3, in which subjects were given more information about their chances of receiving a reward in order to reduce the potential aversiveness of the anticipation.

The differential startle responsiveness at the 9-s probe time between the chance of money and no chance of money trials supports the alternative hypothesis that increased attention to one condition facilitated the response. Participants likely focused more attention on the chance of money trials. Several previous studies involving anticipation of positively valenced stimuli have also found larger startle responses compared to neutral (Nitschke et al. 2002; Sabatinelli et al., 2001) or when anticipating a positive reaction time task (Hamm & Vaitl, 1996; Lipp et al., 1994). For example, Hamm and Vaitl found that during nonaversive conditioning, both CS+ and CS− trials and ITI probes were potentiated when anticipating responding to a rewarded reaction time task. Whereas the two latter studies suggested that increased attentional demands facilitated the response, the former studies argued for an important role of anticipatory arousal.

Interestingly, after the participants learned that they received a match (reward), we found the startle response was significantly smaller compared to when they did not receive a match (nonreward). This finding adds to the corpus of startle research showing that inducing a positive experience (like viewing positively valenced stimuli) can attenuate the startle eyeblink response in contrast to relevant comparison conditions. However, caution is warranted in interpreting this result, as rewarded trials did not induce smaller startle responses than no chance of money trials. The postgoal positive affective experience is thought to lack input from approach processes (Davidson, 1994). Thus, the present findings suggest that an approach component to positive affective stimuli is unnecessary to induce startle suppression.

At the 2-s probe time, magnitudes of eyeblink responses were consistently small. Regardless of whether reward or threat trials, chance of money or no chance trials, the magnitude at this probe time remained consistently small. The most likely explanation is related to the fact that the numbers have just begun to spin and more attention is being paid to the stimuli as part of an orienting response. This phenomenon occurred in all experiments reported herein. The phenomenon of short lead intervals producing inhibited blink responses (e.g., Jennings et al., 1996; Vanman et al., 1996) may be playing a role here as well, even though time of the probe (2 s) is longer than traditional short leads.

In the threat condition, as predicted, participants showed larger eyeblink responses prior to discovering whether they would receive the aversive noise or not compared to safe trials. Evidence for an anticipatory effect of the negative event was bolstered by the results from the feedback probe. When participants were probed after they learned that they would receive the noise, the startle response was significantly larger than even the startle response at the 9-s probe time. These results parallel previous data using threat of shock to induce fear-potentiated startle responses (Grillon et al., 1991, 1993). Thus, for the threat condition, increased size of the startle response likely indicates increased anticipatory anxiety for the potential unpleasant noise blast.

During the ITI period of the threat trials, the few trials when subjects did receive the aversive noise produced smaller startle blinks than either safe or no-noise trials. This effect may be an artifact of the aversive noise itself. In two of the four startle probes administered during the ITI, the aversive noise ran for 3 s, offsetting just 1 s prior to the probe onset. The proximity in time of the high intensity aversive noise may have affected the blink response itself (e.g., due to a refractory effect). Also, this probe time had the most missing responses, due to evasive facial movements (e.g., tensing up) during the noise delivery. Alternatively, the decreased size of the eyeblink could indicate a positive emotional state, such as relief that the noise had stopped.

The lottery paradigm as a whole was successful in inhibiting the startle response to a rewarding stimulus (being told you won money) and in facilitating the startle response to a threatening stimulus (threat of an aversive noise) in comparison to the relevant control conditions. However, the finding of larger startle responses while anticipating a potential reward prompted further investigation. Questioning participants during debriefing highlighted the fact that participants may have been anxious about whether they would win during each chance of money trial. Also increasing their anxiety was the fact that they knew there was always a chance to win a large amount ($20 or $50). In a subsequent experiment, efforts were taken to control for these potential sources of anxiety. To remove some of the uncertainty in Experiment 1, participants in subsequent experiments were provided information about the probability that they would receive a match. Rewards were always the same amount ($1.00) per match instead of a wide-ranging variable amount ($0.50–$50) to reduce the anxiety of knowing they may or may not get a big win.

EXPERIMENTS 2 AND 3: LEVEL OF EXPECTATION OF REWARD AFFECTS STARTLE RESPONSE MAGNITUDE

Participants performed a similar computerized lottery task to the reward trials of Experiment 1 except that their expectations of winning were manipulated. Three colors cued three possible probabilities (low [zero], medium, or high) of winning a trial. Participants received the color cues at the beginning of each trial after digits were entered and their eyeblink startle response was measured at the same four points: two probes during the anticipatory period and one probe during feedback and the ITI periods. Participants learned the color–probability relationships before the trials commenced.

In this experiment, we expected the zero probability trials to be treated similarly as the no chance of money trial in Experiment 1, as the participants would know immediately upon being signaled that they had no chance to win. The medium probability trials matched the chance of money trials in Experiment 1; in both categories participants basically had a 50% chance of winning. We, therefore, predicted that at the 9-s probe time, the medium probability trials would generate the most anxiety and the largest startle response as compared to the low and high probability trials. For the high probability trials, we predicted that participants would show reduced startle responses at the 9-s probe time because the uncertainty and anxiety of receiving a match should decrease, and confidence that they would receive a match should increase. An alternative hypothesis, based on the idea that the different probabilities of matching would induce different levels of attentional resources directed at the stimuli, would predict medium and high probability trials to produce a greater focus of attention than low probability trials and thus facilitate the startle response to a greater extent.

EXPERIMENT 2

Methods

Participants

Forty-six women and 13 men (aged 18–27 years) participated in the experiment. Some participants were dropped due to an insufficient number of startle responses (12) or due to not paying attention to the color–probability relationships (11), leaving 36 participants (29 women, 7 men; mean age = 21.4). Participants were recruited by advertisement and word of mouth. Incentive for participation was the knowledge that money would be won in the experiment. All participants were told, "Most participants win more than $10." Payment for participation was the money "won" (fixed at $36).

General Procedure

As in Experiment 1, participants sat at a monitor, wearing headphones, with three electrodes in standard locations around the left eye and on the forehead. The first block of trials participants received was a "learning block" in which participants played the lottery task to learn the color–probability associations without receiving any monetary rewards. Participants also received nine startle probes to habituate the initial probes. Following this block, participants performed the task for money by entering digits to try to obtain a match as in Experiment 1. Each trial with at least one digit matching won $1.00. At the end of each of the three blocks of trials, participants were paid their winnings. All participants matched on 36 trials of 85 trials in a counterbalanced order. At 2 s into the feedback period of a matching trial (regardless of probability), participants were also provided auditory feedback; they heard a 2-s pleasant noise (an audience gently saying "yea") to further reinforce positive affect. Startle probes were administered at similar times as in Experiment 1: 2 s or 9 s after the digits began spinning (prefeedback probes), or 1.75 s (feedback probe) or 6 s (ITI probe) after receiving feedback. At the end, participants filled out questionnaires concerning their emotional response to the colored trials.

Color-Coded Information

Unlike in Experiment 1, when a trial began in Experiment 2, participants were not told if there was a chance to win money or not. Instead the screen just asked them to "Enter Your Lucky Digits." Upon entering the final digit commencing the bottom row of digits "spinning" as before, a word showing the color name (red, blue, yellow) of the trial popped into center screen and remained until feedback. Participants were told that each of the three colors indicated a different probability of receiving a match. Participants experienced a 0%, 45%, and 90% chance of winning money. During the first block of the trials (learning block), participants were told to pay attention to the colors and report at the end of the block what the probability was for each color in an on-screen estimating task. (The on-screen estimating task consisted of three squares representing each color and participants were asked to "guess the probability that each color resulted in a match." Participants entered their estimates below each color.) Subjects were randomly presented seven trials of each color, matching either 0/7, 3/7, or 6/7 times. The participants' color–probability associations were further confirmed in two ways. The onscreen estimating task was repeated after the final experimental block (participants were unaware of the second color–probability estimation at the end of the experiment until it was presented to them to avoid attempts to mentally track the trials) and a questionnaire was given in which they rated their confidence that each color led to a match. Only relatively accurate participants that paid attention to the color information throughout the experiment (e.g., correctly reported the colors as very low, medium, and very high at the second estimation) were analyzed statistically. Color meaning was counterbalanced across participants using three sets such that each color was presented with each probability. There were no significant differences due to the color set.

Startle probes were presented at the exact same times as in Experiment 1 (2 s, 9 s, feedback probe, or ITI probe) in a counterbalanced order. The number of startle probes delivered was determined by the demands of the winning percentage. For the 0% color trials, six startle probes were delivered during each of the four probe times. For the 45% color trials, seven startle probes were delivered during each of the anticipatory probes (2 s, 9 s) divided into three or four probes for each of the trials that either led to a match or to a nonmatch. During the postfeedback probe times, there were five startle probes delivered during matching 45% color trials, and six startle probes delivered during nonmatching 45% color trials. For the 90% color trials that matched, five startle probes were delivered during each of the four probe times. Finally, there were only four trials in which a subject did not receive a match during a 90% color (the nonrewarding 10%). Thus, the four startle probes were delivered at *either* the feedback or ITI probes counterbalanced across participants.

Self-Report Measures

Shortly after the final block of trials (within 2 min), for each color, participants rated (1 = *not at all*, 7 = *extremely*, Likert scale): "How did you feel while the numbers slowed down and you were about to find out if you got a match or not" on 11 descriptive emotion words (*amused*, *angry*, *anxious*, *aroused*, *disappointed*, *excited*, *happy*, *irritable*, *proud*, *relieved*, *sad*). For each color, participants also rated their "confidence that each color would lead to a match" (1–7 Likert scale, *low–high*).

Apparatus

Control of presentation stimuli and the startle probes were the same as in Experiment 1. The pleasant noise played during a matching trial was a 2-s clip of an audience gently saying "yea" during a performance. The noise was played as a .WAV file, 76–80 dB, with a slow rise time. The sound was from a commercially available sound effects compact disc.

Data Acquisition and Reduction

EMG from the orbicularis oculi was collected and reduced using identical procedures as in Experiment 1. Approximately 14% of eyeblink reflexes were excluded from further analyses due to excessive noise during a 50 ms, prestartle baseline period (e.g., blinks, unusually high amounts of integrated EMG during baseline) or because the onset of the integrated EMG eyeblink reflex began less than 20 ms after the startle probe. Eyeblink reflex magnitudes were *z*-transformed within subjects and within block as before.

Data Analysis

To test hypotheses that the startle blink will be affected by either expecting or receiving a monetary reward, separate repeated measures ANOVAs were used for each probe time. All ANOVAs using a within-subjects factor used a Huynh–Feldt correction where appropriate (Huynh & Feldt, 1970). Participants had the 90%

nonmatching startle probes at either the feedback or ITI probe times but not both. Therefore, startle response for 90% nonmatching probes were not included in the ANOVAs, but were compared to 90% matching trials with paired *t* tests at both feedback and ITI times. These paired *t* tests only included about half the participants at each probe time.

Results

Manipulation Checks

To ensure that participants were paying attention to the colors, they were asked to rate their "confidence" that each color would result in a match. Confidence ratings were (mean, $\pm SD$): 0% color = 1, ± 0; 45% color = 3.89, ± 0.78; 90% color = 6.25, ± 0.55). The mean ratings for each color were significantly different, $F(2,70) = 862$, $p < .0001$, indicating that, overall, participants paid attention to color differences.

Analyses of the emotion ratings based on the color of the trial suggested the probability of reward altered emotional states (Figure 5a). ANOVAs performed on each emotion rating resulted in significant *F* values for all ratings (all $F(2,50)$, ps $< .0001$; even if a Bonferroni correction is made for the 11 tests: new $p = .0045$). As would be expected for the 0% color, participants gave significantly higher ratings for being angry, disappointed, sad, and irri-

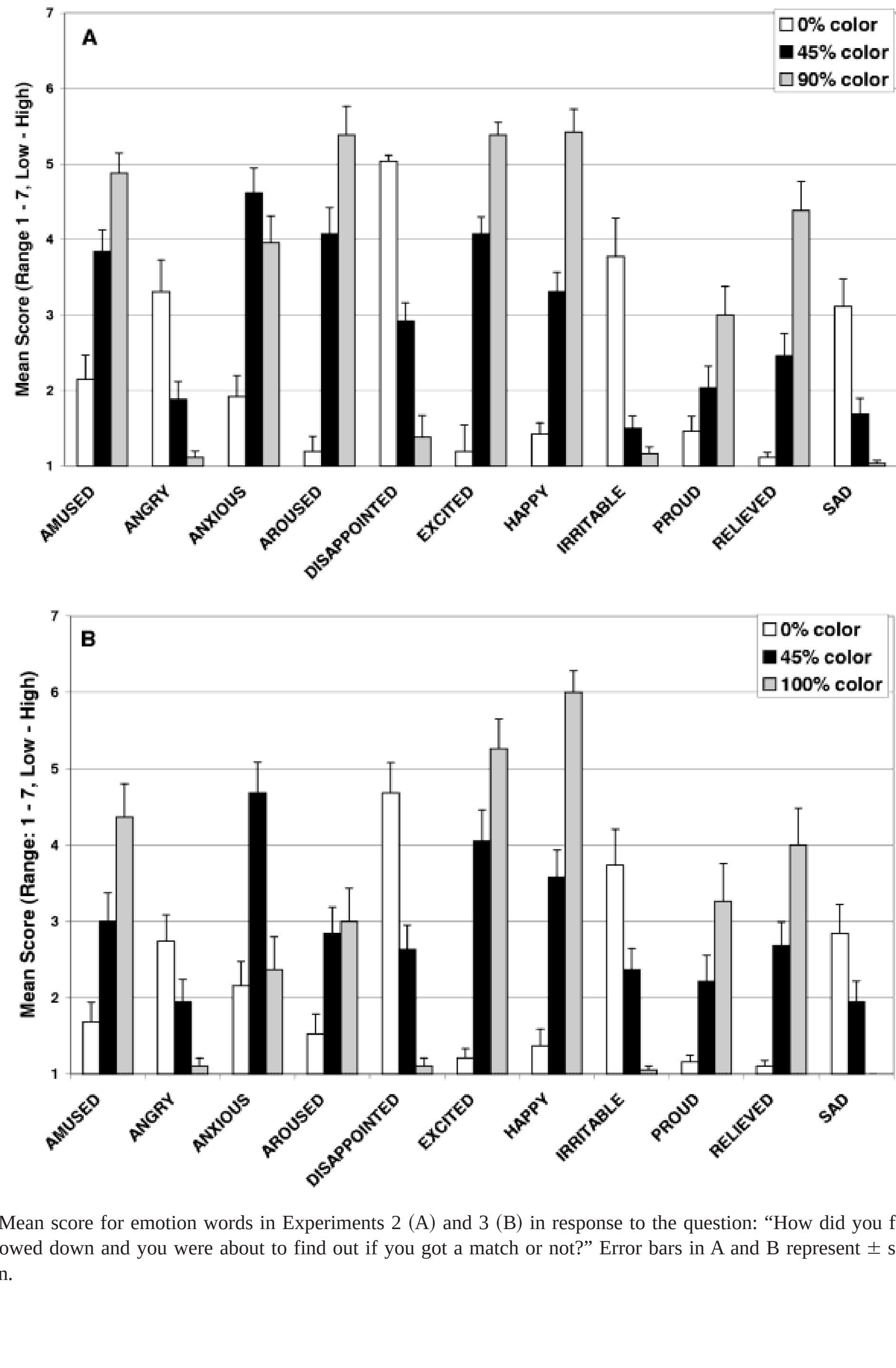

Figure 5. Mean score for emotion words in Experiments 2 (A) and 3 (B) in response to the question: "How did you feel while the numbers slowed down and you were about to find out if you got a match or not?" Error bars in A and B represent ± standard error of the mean.

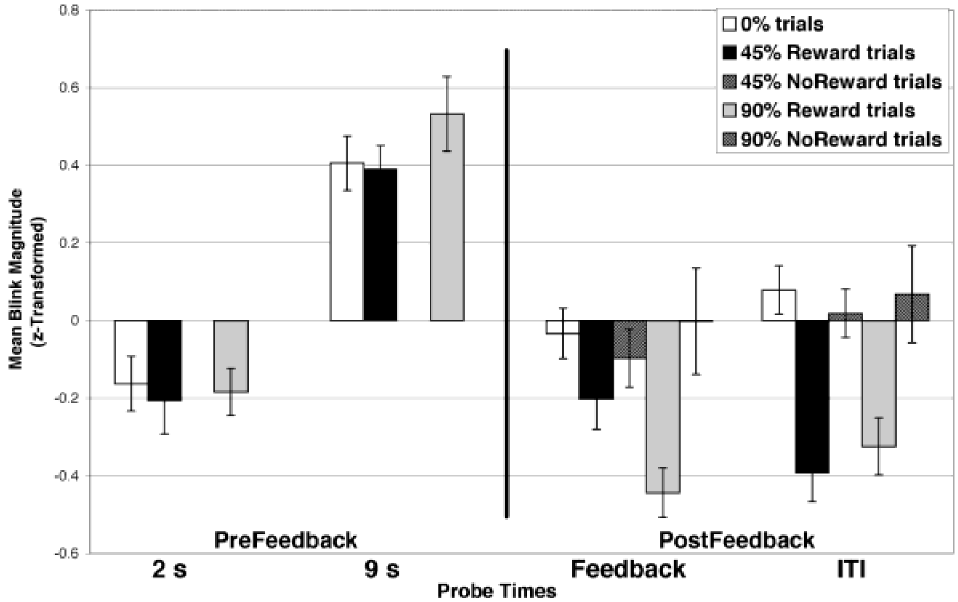

Figure 6. Standardized (z score) eyeblink magnitude averaged for each probe time for each reward condition in Experiment 2. Error bars represent ± standard error of the mean.

table, ps $< .0001$, than for the 45% or 90% colors. The 45% color garnered significantly higher ratings for anxious compared to the 0% color, $p = .0001$. The 90% color showed significantly higher ratings for aroused, excited, happy, relieved, and proud, ps $< .0015$. Surprisingly, ratings for anxious did not differ statistically between the 45% color and 90% color, $p = .071$, and were both significantly greater than for the 0% color, $p = .0004$.

Startle Response: Prefeedback Period[3]

At the 2-s probe time, no significant differences between different color probabilities were seen (Figure 6). And, contrary to what was expected, at the 9-s probe time no significant differentiation of blink magnitudes occurred based on the probability of receiving a reward, $F < 1.0$.

Startle Response: Postfeedback Period (see footnote 3)

Although the different probabilities of winning had little effect during the anticipatory period, during the feedback and ITI periods, the startle blink response was differentiated based on the probabilities of winning and on whether a match occurred or not (Figure 6). At the feedback probe, the ANOVA comparing the four outcomes (0%, 45% match, 45% no match, 90% match) was significant, $F(3,81) = 8.09$, $p = .0002$. Paired comparisons showed that startle magnitude for the 90% color matching trials was significantly smaller than the 0% color, $p < .0001$, and the 45% color matching trials, $p = .002$. Further, a paired t test found significantly smaller blink responses during 90% matching trials than 90% nonmatching trials, $t(14) = 3.45$, $p = .004$. However, startle magnitude for 45% color matching trials did not differ from either 45% nonmatching or 0% color trials, ps $> .18$. As an indication of the possible negative affect induced by not winning a 90% color trial when participants likely expected to win, the 90% nonmatching trials were compared to 0% chance to win and the 45% nonmatching trials. No significant differences were found (90% nonmatching vs. 0%: $t(15) = .58$; 90% nonmatching vs. 45% nonmatching: $t(14) = .40$).

Interestingly, during the ITI, startle eyeblink responses were significantly modulated depending on reward outcome regardless of the probability of winning, $F(3,87) = 13.03$, $p < .0001$. Rewarding trials for both the 45% and 90% colors were significantly reduced as compared to the 0% color, $p < .0001$, $p = .0008$, respectively, and their respective nonrewarding trials, $p < .0001$, paired t-test, $t(16) = 4.03$, $p = .0011$. At the ITI probe that occurred 4.25 s later than the feedback probe, the 45% and 90% colored matching trials were no longer significantly different.

Discussion

Overall, these data indicate a similar pattern to Experiment 1: Startle eyeblink responses were enhanced while participants anticipated receiving feedback concerning a possible reward and were smaller once they received a positive reward as compared to not receiving it. Moreover, presenting participants with three different probabilities to win resulted in a differentiated response to receiving a match (reward). During the feedback period, 1.75 s after learning that they won, participants showed a smaller startle response when it was a trial with the 90% color but not when it was the 45% color. Contrary to our predictions, however, no reliable differentiation in response between the 45% and 90% color matching trials was seen at either the 2-s, 9-s, or ITI probe times. Those

[3] Analyses of the raw data showed the same general significant effects. At the prefeedback probe times, no significant differences for condition were found. At the feedback probe, the 90% color matching trials showed significantly smaller startle magnitude than 0%, $p = .001$, and 45% color matching trials, $p = .024$. The 90% matching trials were also smaller than the 90% nonmatching trials, $p = .04$. The 45% color trials were marginally smaller than the 0%, $p = .061$, and 45% color nonmatching trials, $p = .08$. At the ITI probe, both the 45% and 90% color matching trials produced significantly smaller blinks than 0%, both $p < .0001$, and their respective nonmatching trials (45%: $p < .0001$, 90%: $p = .04$).

trials only differed at the feedback probe when the participants first discover the outcome of a trial. At the 9-s probe time, the 0% colored trials produced startle responses that were no different from the other trials in which there was a chance to win money. With no differences at the 9-s probe time, differential attention to the task did not seem to affect the startle response, and our prediction concerning increased attention was not supported.

At the pregoal 9-s probe time, not only was there a lack of differentiation in startle response, but the 90% colored trials actually tended to show the largest potentiation, in relation to other probes, of the three conditions. This finding is similar to the results of Hamm and Vaitl (1996), who found increased facilitation of startle magnitude while subjects were anticipating either CS+ or CS− conditions during the acquisition period in a nonaversive learning paradigm. One factor that may play a role is some form of anticipatory arousal. High arousal stimuli produced potentiated blink responses in two recent studies (Nitschke et al., 2002; Sabatinelli et al., 2001) which suggests arousal related to anticipation, as in Hamm and Vaitl, is a possible candidate explanation here. Analysis of the self-report scales revealed that the 90% colored trials produced a significant amount of arousal and anxiety in the participants as the spinning digits slowed (Figure 5a). It may be the case that the small amount of uncertainty and subsequent anxiety produced by knowing there was a 10% chance of not winning was enough to influence the participants' arousal levels and their startle response. In Experiment 3, all uncertainty was removed by presenting participants with a set of colored trials that removes all doubt about their chances of winning.

The feedback information was identical when participants received a match and won money, and thus, placed no differential demands on attention directed at the screen. Therefore, the different pattern of suppression of the startle response between the 45% and 90% color matching trials at the feedback probe time can be explained by the different expectations of the participants. During the anticipatory period, participants when presented with the 90% color had 10 s to think about their high likelihood of receiving a match. Thus, they were likely "primed" to expect to win during the 90% trials. During the 45% trials, when participants were confronted with greater uncertainty, there was probably little priming that a reward was imminent. This case is similar to the reward condition in Experiment 1, when there was little differentiation at the feedback probe. The 90% matching trials produced startle responses that were smaller than 90% nonmatching trials. This effect could be due to larger responses in the nonmatching trials from the negative feelings induced when participants did not win when they expected to. However, the 90% nonmatching trials were no different from either 0% trials or from 45% nonmatching trials, suggesting that any negative affect generated from not winning was no different from the other nonmatching trials.

During the ITI, the screen was completely blank so that no differences in attention likely occurred. Yet, at the ITI probe time that occurred 4.25 s after the feedback probe time, both rewarding schedules resulted in smaller startle responses compared to the 0% colored trials or their respective trials in which they did not win. This pattern may be due to the lingering effects of the time course of the positive affect generated by receiving a reward. Specifically, for the 45% colored trials, it may take longer than 1.75 s for the full registration that a winning trial was received if participants were not necessarily expecting to receive a match. One reason why this differentiation of the eyeblink response was more robust in Experiment 2 than in Experiment 1 could be due to increased saliency of the matches with the knowledge of the probabilities of winning.

EXPERIMENT 3

Experiment 3 was conducted to test the prediction that by removing any source of uncertainty or anxiety, the size of the startle response at the 9-s probe time would be reduced by pregoal reward as compared to trials with some level of uncertainty. Thus, participants received three different probabilities of reward as before, except that a 100% colored trial replaced the 90% colored trial. Upon seeing the 100% color, participants should realize that they were going to match on the trial and no feelings of uncertainty would alter their emotional state in a negative direction on those trials.

General Procedure

Procedures were identical to Experiment 2 except the probabilities of winning were changed to 0%, 45%, and 100%. All participants matched on 36 trials of 81 trials in a counterbalanced order.

Participants

Fourteen women and 13 men (aged 18–29 years) participated in the experiment. Some participants were dropped due to an insufficient number of startle responses (4) or due to not paying close attention to the color–probability relationships (3) or due to technical problems (1) leaving 19 participants (11 women, 8 men; mean age = 20.5). Participants were recruited by advertisement and word of mouth. Incentive for participation was the knowledge that money would be won in the experiment. All participants were told, "Most participants win more than $10." Payment for participation was the money "won" (fixed at $36).

Color-Coded Information

The design of the experiment was identical to Experiment 2 except that participants experienced a 0%, 45%, and 100% chance of winning money. During the learning block, participants were presented with seven trials of each color, matching either 0/7, 3/7, or 7/7 times.

Startle probes were presented at the exact same times as in the previous experiments (2 s, 9 s, feedback probe, or ITI probe) in a counterbalanced order. The amount of startle probes delivered was exactly the same as in Experiment 2, except the four 90% color trials in which participants did not receive a match were dropped.

Self-Report

The same self-report measures were administered as in Experiment 2.

Data Acquisition and Reduction

Procedures for acquiring and reducing the data were identical to Experiment 2. Approximately 11% of eyeblink reflexes were excluded from further analyses due to excessive noise during the baseline period or because the onset of the integrated EMG eyeblink reflex began early.

Data Analysis

Analyses identical to Experiment 2 were performed. Between-subject *t* tests were used to compare confidence ratings and emo-

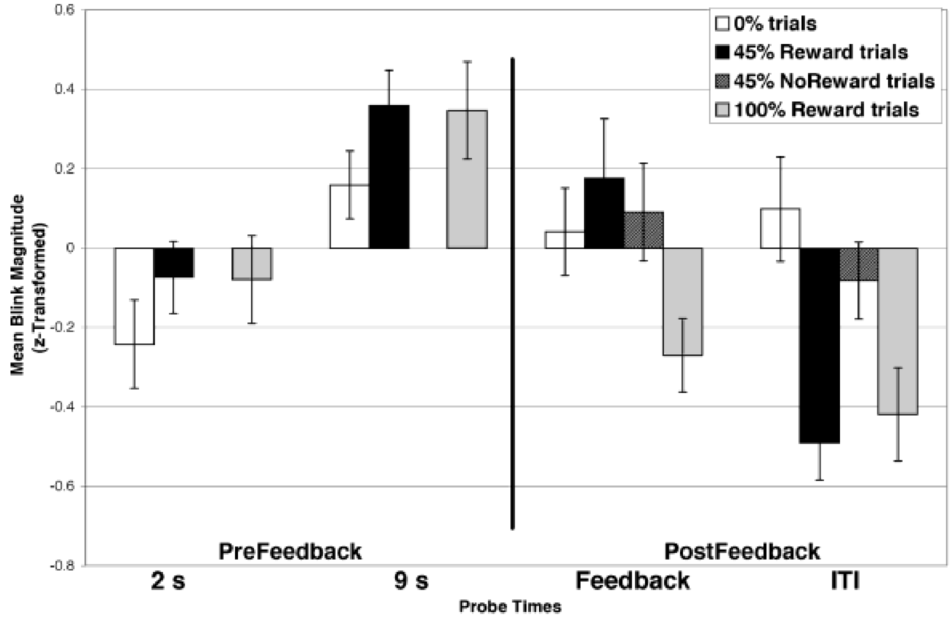

Figure 7. Standardized (*z* score) eyeblink magnitude averaged for each probe time for each reward condition in Experiment 3. Error bars represent ± standard error of the mean.

tion ratings for the 90% and 100% colored trials and eyeblink magnitude between Experiments 2 and 3.

Results

Manipulation Checks

Confidence ratings were (mean, $\pm SD$): 0% color = 1, ±0; 45% color = 3.37, ±1.01; 100% color = 6.84, ±0.69). The mean ratings for each color were significantly different, $F(2,36) = 234$, $p < .0001$, bolstering the claim that, overall, participants paid attention to the different color probabilities. Comparing the confidence ratings between the 90% color (Experiment 2) and the 100% color revealed that the mean rating for confidence that participants would receive a match significantly increased when the 100% color was used, $t(43) = 3.41$, $p = .0014$.

As in Experiment 2, analyses of the emotion ratings based on the color of the trial suggested the probability of reward altered emotional states. The pattern of significant effects was identical to Experiment 2 (with the same Bonferroni correction) with only two notable exceptions (compare Figure 5a to 5b). For ratings of anxious, the 45% color was significantly greater than both the 0% and 100% colors, ps $< .0008$, whereas ratings for the 100% color were low and statistically equal to that of the 0% color, $p > .05$. Ratings for aroused for both the 45% and 100% colors were significantly greater than for the 0% color, ps $= .0015$, but unlike in Experiment 2, were equal to each other, $p > .05$. Ratings for the categories of anxious and aroused across experiments were compared when the probability of the color was altered from 90% to 100%. Ratings of anxious were significantly reduced when the color had a 100% probability as compared to a 90% probability (100% mean, $\pm SD$: 2.63, ±2.04; 90%: 3.94, ±1.86; $t(57) = 2.57$, $p = .013$). Ratings for aroused did not differ by probability, $p > .05$.

Startle Response: Prefeedback Period[4]

As in Experiment 2, no differences in startle blink magnitude based on color probability were detected at the 2-s probe time, $F < 1.0$ (Figure 7). Again, similar to Experiment 2, an ANOVA for startle blink magnitude at the 9-s probe time revealed no significant differences based on color probability, $F(2,36) = 1.43$, $p = .25$. The lack of a main effect for condition at the 9-s probe time is surprising considering the significant decrease in the ratings for anxious compared to Experiment 2 and the use of the 100% probability. Subjects knew when the color first appeared that they would receive a reward that trial. Between-group comparisons across Experiments 2 and 3 were made with the 0% color trials, the 90% color trials, and the 100% color trials for startle blink magnitude at the 9-s probe time. Although the *z* scores for startle blink magnitude were comparatively smaller in Experiment 3 as in Experiment 2 for both the 0% and 100% color trials, only the reduction in the magnitude for the 0% color was significant (0% color: $t(52) = 2.06$, $p = .044$; 100% color: $t(52) = 1.39$, $p = .17$).

Startle Response: Postfeedback Period (see footnote 4)

Generally replicating Experiment 2, at the feedback probe time, the probabilities of receiving a reward marginally affected the

[4]Analyses of the raw data showed the same general significant effects. At the 9-s prefeedback probe time, a marginally significant effect for condition was found: the 0% color trials showed smaller blinks than the 45%, $p = .054$, and 100%, $p = .06$, matching trials. At the feedback probe, the 100% color matching trials showed marginally smaller startle magnitude than 0%, $p = .06$, and 45% color matching trials, $p = .14$. The 45% matching trials were not different from other conditions. At the ITI probe, both the 45% and 100% color matching trials produced significantly smaller blinks than 0%, $p = .016$, $p = .007$, respectively, and the 45% matching trials produced significantly smaller blinks than the 45% nonmatching trials, $p = .005$.

startle blink response, $F(3,48) = 2.60$, $p = .063$ (Figure 7). Paired comparisons showed that the 100% color had significantly smaller startle blink magnitude compared to either the 0% color trials, $p = .032$, or the 45% matching trials, $p = .015$. Blink magnitude for the 45% color when matching did not differ from either 45% nonmatching or 0% color trials, $p\text{s} > .05$.

The startle responses during the ITI indicated an identical pattern for the 100% color as found previously for the 90% color. Startle blink responses were significantly modulated depending on reward outcome, $F(3,51) = 6.24$, $p = .002$. Both the 45% color matching trials and the 100% color were significantly suppressed compared to the 0% color trials, $p = .005$, $p = .003$, respectively. Additionally, the 45% color matching trials were significantly reduced compared to the nonmatching trials, $p < .003$. Startle responses to the 45% and 100% colored trials were equivalent.

Discussion

Altering the probability of receiving a reward from 90% to 100% had the desired effect of reduced ratings of anxiety and arousal and increased the confidence that a match would be obtained and a monetary reward received. Although, relative to other probes, the magnitude of the startle response at the 9-s probe time decreased using a 100% probability color versus a 90% probability color, the difference was not reliable. Thus, the level of reward expectation had little effect at the moment when anticipation was at its pregoal attainment peak (9-s probe). Based on the hypothesis that attention may be directed at trials with different consequences (no, medium, or high chance to win) differently, the prediction that differences would be found between the 45% and 100% color trials and 0% trials in startle responsivity was also not supported in this sample. The data during the postfeedback period were consistent with Experiment 2: At the feedback probe, relatively smaller startle eyeblinks were found only for the high probability color (100%) and not the middle probability color (45%). At the ITI probe, the data revealed the same exact pattern as in Experiment 2. Six seconds following the presentation of the reward information, smaller startle eyeblink magnitudes were found during matching (winning) trials versus nonmatching trials, suggesting again that positive affect generated by receiving the reward has a lasting time course, in the range of seconds. The results also confirm the finding from Experiment 2 that matching on a 45% trial seems to take longer to influence the magnitude of the startle response than high probability trials when participants may be primed to expect a reward.

Given that differentiation between positive- and negative-valenced pictures has been found during very short lead intervals ($<$500 ms; Codispoti et al., 2001; Vanman et al., 1996), it is surprising that no differentiation occurred at the 2-s probe time. When the digits began to spin, the color word appeared and if the color represented 100% (or 0%), the participants knew immediately that they would win another reward (or not). By the time of the probe, participants had known for 2,000 ms that they had won the trial or had no chance to win, yet no differences were found.

General Discussion

Two patterns of response to receiving a reward emerged in the present paradigm. At the peak of an anticipatory period, when one was about to learn the outcome of a potential reward trial (pregoal), an acoustic probe producing a startle response induced large eyeblink responses regardless of condition. In contrast, after learning that one has received a reward (postgoal), that same acoustic probe produced a smaller response that was modulated by the expectation of receiving that reward. Reward trials with higher initial expectations of matching produced blinks that were smaller than trials with no rewards either due to not matching or when there were no expectations to receive a reward. When it was difficult to predict the reward outcome, the results were variable immediately following reward feedback information, but showed a similar pattern to trials with higher reward expectations seconds later.

This pattern of findings ran counter to predictions that approach-related positive affect (namely, pregoal attainment positive affect) would generate strong inhibitory effects on the startle response. Instead, we found the stronger effects of postgoal attainment positive affect in suppressing the startle response compared to trials that did not induce positive affect. This type of positive affect likely does not reflect the activity of an approach system in the brain (Davidson, 1994, 1998), but rather is tied to processes associated with consummatory responses.

In previous studies to test for reward-attenuated startle responsiveness, Koch and colleagues (Koch et al., 1996; Schmid et al., 1995) found that startling a rat when it was presented with a reliable signal for desirable food suppressed the whole-body startle response. These rodent studies can be directly compared to Experiment 3, in which participants were provided with a reliable signal (100% color) indicating they would receive a desirable object ($1.00). However, when presented with a reward signal, the human eyeblink startle response was potentiated, not attenuated relative to the comparison conditions. This discrepancy is unlikely to be due to differences in response measures (whole-body vs. eyeblink). Ultimately, these findings may be influenced by the nature of the anticipation itself, potentially overriding the effects of induced positive affect.

Studies that have used warning signals to indicate the valence of an upcoming stimulus have shown similar effects. Putnam and Vanman (1999) suggested that for long lead stimuli, the attention or orienting processes during anticipation of an event contributes to facilitating a potentiated startle response. Hamm and Vaitl (1996) also found potentiation in anticipation of both potential reward and nonreward trials. If similar attentional processes were induced in the current lottery paradigm, the pattern of potentiated eyeblink magnitude during anticipation at the 9-s probe time may be explained. A recent study in this laboratory used warning signals to alert participants to the valence of upcoming affectively valenced slides. Startle probes presented during the stimuli that warned of positively valenced pictures also showed larger startle eyeblink responses than during warning of neutrally valenced pictures (Nitschke et al., 2002; see also Sabatinelli et al., 2001). These data were comparable to the 100% colored trials in Experiment 3 and may result from a similar process.

Lipp et al. (1997) suggested attention to a signal indicating a chance to win money may induce arousal. The Sabatinelli and Nitschke studies also found evidence for an arousal effect such that pictures rated highest on arousal, regardless of valence, produced larger startle blinks than low arousal stimuli. Sabatinelli et al. (2001) suggested that large startle responses found during the anticipation of viewing erotic (positive) stimuli were due to the arousing quality of the stimuli. However, reports showing increases in arousal level increasing the suppressive effects of positive stimuli (Cuthbert et al., 1996; Koukounas & Over, 2000) and the present data suggest a simple analysis of arousal may be inadequate to understand this phenomenon. The 9-s probe comes at a point when one might expect the maximal anticipatory arousal. This arousal may result from the integration of feelings of excitement (i.e., being excited at the prospect of receiving the reward, especially in high-probability trials), uncertainty, and anxiety of the possibility of not winning the reward. Concurring with this notion, when the 90% probability colored trials were switched to 100% colored trials, ratings for arousal decreased such that they were no longer significantly greater than ratings for the 45% colored trials. Yet in both Experiments 2 and 3, participants consistently rated exciting the highest for both high probability colored trials and showed potentiated startle responses. Thus, lower ratings of arousal did not correspond to suppressed startle responses during the anticipatory period. Previous studies examining startle responses with participants passively viewing stimuli may not have generated the type of arousal produced by anticipation of a desired reward.

A novel finding from this study is the effect of receiving a winning match on postfeedback period startle responses. Although a previous study (Spence & Cook, 1993) found no effects of reward feedback in a reaction time task, we found startle blinks were smaller on reward trials than nonreward trials, especially when the participants had knowledge of the likelihood of obtaining a reward. Three seconds after the offset of feedback about the trial outcome, differential blink responses, based on reward outcome, were still evident. Although it is possible that the different conditions invoked different amounts of attention directed at the stimuli on-screen, there are several lines of evidence that suggest that for this particular effect, attention is not likely to play a strong role. Recent studies by Lipp et al. (1997, 1998, 2000) have shown that attention directed to a task-relevant stimulus facilitates startle magnitude compared to a task-irrelevant stimulus. If trials with an increased opportunity for reward garner greater attention, we would expect them to produce larger blink responses rather than smaller. Startle probes delivered during the ITI come several seconds after the screen has gone blank. Attention to visual feedback information ended and we find strong differences between rewarded and nonrewarded trials. Finally, several studies have found either a shift over time in the effects of attentional and affective cues, with attentional effects occurring earlier and affect showing influences later (Bradley et al., 1999), or have found that startle eyeblink inhibition occurs at short lead intervals and startle facilitation at long lead intervals (Jennings et al., 1996). The former effect fits well with our findings, but the latter effect does not. We did not find facilitation at longer lead times with the rewarded (the likely attended to) trials, but smaller blink sizes.

The sensory modalities of the stimuli and the startle probe used have been proposed to be an important factor modulating startle responsiveness (Hackley, 1999; Lipp et al. 2000; Putnam & Vanman, 1999). However, there are inconsistencies in the literature about the effects of matching versus mismatching stimulus and startle probe modalities on startle response and on task demand effects. For example, Lipp et al. only found strong differences between visual and auditory stimuli affecting startle responses using reaction time tasks (2000), not with discrimination tasks (1997, 1998). Thus, the role of modality modulating these effects is complicated by other aspects of the experimental tasks, such as the motor preparedness necessary during reaction time tasks. Traditional attention theories suggested that startle magnitude is facilitated when subjects attend to the modality in which the startle-eliciting stimulus is presented but is inhibited when attending to a different modality. Recent studies by Filion, Dawson, and Schell (1993), Lipp et al. (1994, 1997, 1998, 2000), and work with emotion modulated startle (Bradley et al., 1999) have shown that modality effects can be modified or overshadowed by different attentional and affective influences.

In this set of experiments, startle responses were modulated by several different sources. Receiving a matching trial resulting in winning a monetary reward decreased the startle response presumably by changes in concomitant emotions. While participants anticipated receiving feedback, attentional effects related to anticipatory arousal likely facilitated startle responses regardless of the emotions invoked. When the aversive noise was delivered in a matching threat trial, anticipatory anxiety likely facilitated startle responses once participants were told the aversive event was imminent. Although these three mechanisms all impacted the startle response in different ways and have different underlying neurocircuitries, they all have in common connections to brainstem nuclei (specifically, the caudal pontine reticular nucleus; Koch, 1999). Given the variability across studies in the approach to assessing affective modulation of the startle response, the current data suggest that startle responsivity may not be an appropriate blanket measure of all types of affect (Lang, 1995; Lipp et al., 1997; Putnam & Vanman, 1999).

In sum, this lottery paradigm successfully showed eyeblink startle response differences to winning and not winning a reward (money) and a potentiation of eyeblink startle to the threat of a negative event (aversive noise blast). In the former case, the postgoal rather than pregoal attainment of a reward likely caused the attenuation of the startle eyeblink responses. It may be that any anticipation facilitates the startle response regardless of the affective valence of the organism at the time. The physiological mechanisms of this anticipation effect have yet to be elucidated. Further studies are needed using positively valenced stimuli to address how positive affect influences neurophysiology and to adequately place the present study involving reward in the appropriate context. The startle response is but one measure that seems to differentiate positive and negative emotions, but more studies are required to better understand this differentiation.

REFERENCES

Allen, N. B., Wong, S., Kim, Y., & Trinder, J. (1996). Startle reflex and heart rate responses during appetitive and aversive anticipation. *Psychophysiology, 33*, S18.

Bradley, M. M., Cuthbert, B. N., & Lang, P. J. (1990). Startle reflex modification: Emotion or attention? *Psychophysiology, 27*, 513–522.

Bradley, M. M., Cuthbert, B. N., & Lang, P. J. (1996). Lateralized startle probes in the study of emotion. *Psychophysiology, 33*, 156–161.

Bradley, M. M., Cuthbert, B. N., & Lang, P. J. (1999). Affect and the startle reflex. In M. E. Dawson, A. M. Schell, & A. H. Böhmelt (Eds.), *Startle modification: Implications for neuroscience, cognitive science, and clinical science* (pp. 157–183). Cambridge, UK: Cambridge University Press.

Bradley, M. M., & Lang, P. J. (2000). Affective reactions to acoustic stimuli. *Psychophysiology, 37*, 204–215.

Codispoti, M., Bradley, M. M., & Lang, P. J. (2001). Affective reactions to briefly presented pictures. *Psychophysiology, 38*, 474–478.

Cook, E. W., III, Hawk, L. W., Davis, T. L., & Stevenson, V. E. (1991). Affective individual differences and startle reflex modulation. *Journal of Abnormal Psychology, 100*, 3–13.

Cuthbert, B. N., Bradley, M. M., & Lang, P. J. (1996). Probing picture perception: Activation and emotion. *Psychophysiology, 33*, 103–111.

Cuthbert, B. N., Schupp, H. T., Bradley, M. M., McManis, M., & Lang, P. J. (1998). Probing affective pictures: Attended startle and tone probes. *Psychophysiology, 35*, 344–347.

Davidson, R. J. (1994). Asymmetric brain function, affective style, and psychopathology: The role of early experience and plasticity. *Development and Psychopathology, 6*, 741–758.

Davidson, R. J. (1998). Affective style and affective disorders: Perspectives from affective neuroscience. *Cognition and Emotion, 12*, 307–330.

Davidson, R. J., & Irwin, W. (1999). The functional neuroanatomy of emotion and affective style. *Trends in Cognitive Sciences, 3*, 11–21.

Dawson, M. E., Schell, A. M., & Böhmelt, A. H. (1999). *Startle modification: Implications for neuroscience, cognitive science, and clinical science.* Cambridge, UK: Cambridge University Press.

Ehrlichman, H., Brown, S., Zhu, J., & Warrenburg, S. (1995). Startle reflex modulation during exposure to pleasant and unpleasant odors. *Psychophysiology, 32*, 150–154.

Ehrlichman, H., Brown Kuhl, S., Zhu, J., & Warrenburg, S. (1997). Startle reflex modulation by pleasant and unpleasant odors in a between-subjects design. *Psychophysiology, 34*, 726–729.

Erickson, L. M., Levenston, G. K., Curtin, J. J., Goff, A. B., & Patrick, C. J. (1995). Affect and attention in startle modulation: Picture perception and anticipation. *Psychophysiology, 32*, S30.

Filion, D. L., Dawson, M. E., Schell, A. M. (1993). Modification of the acoustic startle-reflex eyeblink: A tool for investigating early and late attentional processes. *Biological Psychology, 35*, 185–200.

Grillon, C., Ameli, R., Merikangas, K., Woods, S. W., & Davis, M. (1993). Measuring the time course of anticipatory anxiety using the fear-potentiated startle reflex. *Psychophysiology, 30*, 340–346.

Grillon, C., Ameli, R., Woods, S. W., Merikangas, K., & Davis, M. (1991). Fear-potentiated startle in humans: Effects of anticipatory anxiety on the acoustic blink reflex. *Psychophysiology, 28*, 588–595.

Hackley, S. A. (1999). Implications of blink reflex research for theories of attention and consciousness. In M. E. Dawson, A. M. Schell, & A. H. Böhmelt (Eds.), *Startle modification: Implications for neuroscience, cognitive science, and clinical science* (pp. 137–156). Cambridge, UK: Cambridge University Press.

Hamm, A. O., & Vaitl, D. (1996). Affective learning: Awareness and aversion. *Psychophysiology, 33*, 698–710.

Huynh, H., & Feldt, L. S. (1970). Conditions under which means square ratios in repeated measurements designs have exact *F*-distributions. *Journal of the American Statistical Association, 65*, 1582–1589.

Ikemoto, S., & Panksepp, J. (1999). The role of nucleus accumbens dopamine in motivated behavior: A unifying interpretation with special reference to reward-seeking. *Brain Research Reviews, 31*, 6–41.

Jansen, D. M., & Frijda, N. H. (1994). Modulation of the acoustic startle response by film-induced fear and sexual arousal. *Psychophysiology, 31*, 565–571.

Jennings, P. D., Schell, A. M., Filion, D. L., & Dawson, M. E. (1996). Tracking early and late stages of information processing: Contributions of startle eyeblink reflex modification. *Psychophysiology, 33*, 148–155.

Knutson, B., Fong, G. W., Adams, C. M., Varner, J. L., & Hommer, D. (2001). Dissociation of reward anticipation and outcome with event-related fMRI. *NeuroReport, 12*, 3683–3687.

Koch, M. (1999). The neurobiology of startle. *Progress in Neurobiology, 59*, 107–128.

Koch, M., Schmid, A., & Schnitzler, H.-U. (1996). Pleasure-attenuation of startle is disrupted by lesions the nucleus accumbens. *NeuroReport, 7*, 1442–1446.

Koukounas, E., & Over, R. (2000). Changes in the magnitude of the eyeblink startle response during habituation of sexual arousal. *Behaviour Research and Therapy, 38*, 573–584.

Lang, P. J. (1995). The emotion probe: Studies of motivation and attention. *American Psychologist, 50*, 372–385.

Lang, P. J., Bradley, M. M., & Cuthbert, B. N. (1990). Emotion, attention, and the startle reflex. *Psychological Review, 97*, 377–395.

Larson, C. L., Ruffalo, D., Nietert, J. Y., & Davidson, R. J. (2000). Temporal stability of the emotion-modulated startle response. *Psychophysiology, 37*, 92–101.

Lipp, O. V., Sheridan, J., & Siddle, D. A. T. (1994). Human blink startle during aversive and nonaversive Pavlovian conditioning. *Journal of Experimental Psychology: Animal Behavior Processes, 20*, 380–389.

Lipp, O. V., Siddle, D. A. T., & Dall, P. J. (1997). The effect of emotional and attentional processes on blink startle modulation and on electrodermal responses. *Psychophysiology, 34*, 340–347.

Lipp, O. V., Siddle, D. A. T., & Dall, P. J. (1998). Effects of stimulus modality and task condition on blink startle modulation and on electrodermal responses. *Psychophysiology, 35*, 452–461.

Lipp, O. V., Siddle, D. A. T., & Dall, P. J. (2000). The effect of warning stimulus modality on blink startle modification in reaction time tasks. *Psychophysiology, 37*, 55–64.

Manber, R., Allen, J. J. B., Burton, K., & Kaszniak, A. W. (2000). Valence-dependent modulation of psychophysiological measures: Is there consistency across repeated testing? *Psychophysiology, 37*, 683–692.

Miltner, W., Matjak, M., Braun, C., Diekmann, H., & Brody, S. (1994). Emotional qualities of odors and their influence on the startle reflex in humans. *Psychophysiology, 31*, 107–110.

Nitschke, J. B., Larson, C. L., Smoller, M. J., Navin, S. D., Pederson, A. J. C., Ruffalo, D., Mackiewicz, K. L., Gray, S. M., Victor, E., & Davidson, R. J. (2002). Startle potentiation in aversive anticipation: Evidence for state but not trait effects. *Psychophysiology, 39*, 254–258.

Putnam, K. M., Gooding, D. C., Larson, C. L., Jackson, D. C., & Davidson, R. J. (1999). Indicators of the emotional experience of anhedonia: Emotion-modulated startle and resting EEG. *Psychophysiology, 36*, S92.

Putnam, L. E., & Vanman, E. J. (1999). Long lead interval startle modification. In M. E. Dawson, A. M. Schell, & A. H. Böhmelt (Eds.), *Startle modification: Implications for neuroscience, cognitive science, and clinical science* (pp. 72–92). Cambridge, UK: Cambridge University Press.

Sabatinelli, D., Bradley, M. M., & Lang, P. J. (2001). Affective startle modulation in anticipation and perception. *Psychophysiology, 38*, 719–722.

Schmid, A., Koch, M., & Schnitzler, H.-U. (1995). Conditioned pleasure attenuates the startle response in rats. *Neurobiology of Learning and Memory, 64*, 1–3.

Spence, E. L., & Cook, E. W., III. (1993). Modulation of startle by attention but not emotion in an appetitive reaction time task. *Psychophysiology, 30*, S62.

Sutton, S. K., Davidson, R. J., Donzella, B., Irwin, W., & Dottl, D. (1997). Manipulating affective state using extended picture presentations. *Psychophysiology, 34*, 217–226.

van Boxtel, A., Boelhouwer, A. J. W., & Bos, A. R. (1998). Optimal EMG signal bandwidth and interelectrode distance for the recording of acoustic, electrocutaneous, and photic blink reflexes. *Psychophysiology, 35*, 690–697.

Vanman, E. J., Boehmelt, A. H., Dawson, M. E., & Schell, A. M. (1996). The varying time course of attentional and affective modulation of the startle eyeblink reflex. *Psychophysiology, 33*, 691–697.

Vrana, S. R. (1995). Emotional modulation of skin conductance and eyeblink responses to a startle probe. *Psychophysiology, 32*, 351–357.

Vrana, S. R., Spence, E. L., & Lang, P. J. (1988). The startle probe response: A new measure of emotion? *Journal of Abnormal Psychology, 97*, 487–491.

(Received April 1, 2001; Accepted June 19, 2002)