ABSTRACT—For humans, the threat of painful shock greatly potentiates the reflexive startle blink. Moreover, viewing unpleasant, compared with pleasant, pictures also prompts heightened startle reflexes, suggesting that the startle reflex indexes general defensive activation. In this study, pleasant or unpleasant pictures were used to signal shock threat in order to explore how previous affective associations modulate new defensive reactions. When cuing threat of shock, pleasant and unpleasant pictures prompted physiological profiles consistent with defensive activation, indicating that threat of shock renders previously pleasant cues aversive. For unpleasant pictures only, defensive startle was potentiated even when these cues signaled safety. Taken together, the data indicate that (a) regardless of their intrinsic affective meaning, cues signaling shock threat prompt somatic and autonomic reactions consistent with defense, and that (b) intrinsically unpleasant cues continue to prompt defensive activation even when the context of their presentation is specifically nonthreatening.

When confronting cues that predict an imminent painful shock, both people (Hamm, Greenwald, Bradley, & Lang, 1993) and rats (Davis, 1989) show an enhanced startle reflex. Furthermore, Grillon and Davis (e.g., Grillon, Ameli, Woods, Merikangas, & Davis, 1991; Grillon & Davis, 1995) have shown repeatedly that for humans, the mere verbal threat of electric shock is enough to produce the same effect. That is, the reflexive blink response is potentiated when startle probes are presented in the context of a cue (e.g., a red light—“threat”) that signals the possibility of electric shock relative to when they are presented in the context of a cue (e.g., a green light—“safe”) signaling that no shocks will be delivered.

In humans, the startle reflex is similarly potentiated when people look at unpleasant pictures (see Bradley, Cuthbert, & Lang, 1999, for a review). Moreover, the startle reflex is inhibited when people view pleasant scenes, compared with affectively neutral pictures. In effect, the hedonic valence of stimuli—that is, how pleasant or unpleasant they are—can be determined by the magnitude of concurrently elicited startle blinks.

We have interpreted affective modulation of the startle reflex as an instance of motivational priming. In this view (see Koons, 1967; Lang, Bradley, & Cuthbert, 1990, 1997), emotions are organized motivationally—by a defensive motivational system, activated in contexts involving threat, and an appetitive system, activated in contexts that sustain the organism, promoting survival. These systems are implemented through neural circuits in the brain that are old in evolution and shared across mammalian species. According to the motivational-priming view, activation of the defense system by an unpleasant cue (i.e., a shock or unpleasant picture) primes related defensive reflexes such as the startle response; conversely, when the appetitive system is predominant, defensive reflexes are inhibited.

Thus, threat of shock activates the defensive motivational system, potentiating the startle reflex. In the absence of shock threat, pleasant and unpleasant cues are presumed to intrinsically activate the appetitive and defensive motivational systems, prompting startle enhancement or inhibition, respectively. In the current study, we used pleasant or unpleasant pictures to cue threat of shock (or safety) in order to investigate how existing hedonic associations modify reactions to upcoming aversive events. In the classical threat-of-shock paradigm (e.g., Grillon et al., 1991), the critical comparison is between the magnitude of startle reflexes elicited during cues that signal threat of shock (threat period) and the magnitude of startle reflexes elicited during cues that signal a period that is free of shock threat (safe period). In the present experiment, we examined these startle effects as a function of the hedonic valence of the cue and, in addition to startle, assessed other concurrent defensive reactions (e.g., in heart rate, facial muscle action) that are prompted by threat.

One hypothesis is that when pleasant pictures cue shock, concurrent appetitive activation will lead these cues to prompt
weaker defensive reactions than occur when unpleasant cues signal shock threat. This reciprocal-activation hypothesis is somewhat supported by counterconditioning studies suggesting that it is difficult to change associations from aversive to appetitive (e.g., Bromage & Scavio, 1978; Scavio, 1974) or vice versa. However, it is also possible that cues signaling threat of shock will potentiate the startle reflex, compared with cues that signal safety, regardless of the a priori hedonic valence of the cues. According to this defensive-activation hypothesis, once a cue signals an aversive event (such as the possibility of painful shock), the defense system is activated, regardless of prior hedonic associations. This hypothesis predicts that picture cues threatening shock, regardless of whether they are pleasant or unpleasant, will elicit larger somatic and autonomic reflexes than do cues signaling safety. Both hypotheses predict that in the absence of shock threat, reflexes should be potentiated when people view unpleasant, compared with pleasant, pictures, as these aversive stimuli should continue to activate the defense system.

In the present study, threat and safety cues consisted of a variety of different pictures, selected from the International Affective Picture System (IAPS; Lang, Bradley, & Cuthbert, 2001), that are rated either as highly pleasant and arousing or as highly unpleasant and arousing; people reliably react to these pictures with affective differentiation (e.g., Bradley, Codispoti, Cuthbert, & Lang, 2001; Lang, Greenwald, Bradley, & Hamm, 1993). Half of the participants were told that if any pleasant picture was presented, presentation of an electric shock was possible when they viewed pleasant pictures; 16 participants were instructed that shock was possible when they viewed pleasant pictures (threat-unpleasant group), and not when they viewed pleasant pictures; 16 participants were instructed that shock was possible when they viewed pleasant pictures (threat-pleasant group). Because of equipment or experimenter error, some data were lost for some participants. The final Ns were 30 for the analysis of startle, 28 for the analysis of skin conductance and heart rate (14 in the threat-pleasent group), and 27 for the analysis of corrugator EMG activity (14 in the threat-pleasant group). Approximately half of the participants who provided data for each measure in each group were female.

### PHYSIOLOGICAL MEASURES OF DEFENSIVE ACTIVATION

Fear-potentiated startle is one index of defensive activation. In a normal picture-viewing context, unpleasant (compared with pleasant) pictures also prompt increased cardiac deceleration (similar to the fear bradycardia observed in animals; see Campbell, Wood, & McBride, 1997) and heightened activity over the corrugator facial (“frown”) muscle (Bradley et al., 2001; Lang et al., 1993; Winton, Putman, & Krauss, 1984). To the extent that threat of shock prompts defensive activation (as opposed to sheer anticipatory processing, e.g.), cues signaling threat of shock are expected to prompt enhanced cardiac deceleration and increased corrugator electromyographic (EMG) activity. To date, there is limited understanding of the pattern of autonomic and somatic physiological changes that might accompany startle modulation under threat of shock.

Unlike cardiac and facial EMG measures, skin conductance activity does not discriminate between defensive and appetitive activation in a normal picture-viewing context. Rather, both unpleasant and pleasant pictures prompt greater electrodermal reactions than neutral pictures (Lang et al., 1993), suggesting that sympathetic activity increases during viewing of emotional pictures. Moreover, Öhman, Hamm, and Hugdahl (2000) noted that skin conductance activity increases for signaling stimuli, regardless of whether they cue aversive (e.g., shock) or non-aversive (reaction time task) events, suggesting that this measure also reflects the signal value of the cue. In the case of the present study, skin conductance would be heightened for cues that threaten shock, compared with cues that signal safety, regardless of their a priori hedonic valence.

### METHOD

#### Participants

Thirty students (14 female) participated in partial fulfillment of a requirement for the general psychology class at the University of Florida; the study was approved by the University of Florida Institutional Review Board. Fourteen participants received instructions that an electric shock could occur when they viewed unpleasant pictures (threat-unpleasant group), and not when they viewed pleasant pictures; 16 participants were instructed that shock was possible when they viewed pleasant pictures (threat-pleasant group).

Because of equipment or experimenter error, some data were lost for some participants. The final Ns were 30 for the analysis of startle, 28 for the analysis of skin conductance and heart rate (14 in the threat-pleasent group), and 27 for the analysis of corrugator EMG activity (14 in the threat-pleasant group). Approximately half of the participants who provided data for each measure in each group were female.

#### Materials and Design

Pictures were selected from the IAPS (Center for the Study of Emotion and Attention, 2001) on the basis of their normative pleasure and arousal ratings (Lang et al., 2001). Twelve pictures, half pleasant and half unpleasant, were presented to each participant. They were selected from a set of 36.\(^1\) to provide generalizability of the results beyond a small set of materials.

The presentation of stimuli and the recording of responses were controlled using a Northgate IBM-compatible computer running VPM experimental control software (Cook, 2001). Pictures were presented for 6 s each (with a 6- to 10-s intertrial interval) using a Kodak Ektographic III AM slide projector fitted with a Gerbrands 61166 shutter. Startle responses were elicited by a 50-ms, 95-dB (A) burst of white noise delivered between 2 and 4 s after picture onset. Four startle probes were also delivered during the intertrial intervals.

\(^1\)The pleasant pictures (identified by IAPS number) were 1440, 1460, 1540, 1710, 1730, 1920, 2070, 4641, 4660, 5010, 7290, 7330, 8162, 8200, 8350, 8470, 8501, and 8510; the unpleasant pictures were 1120, 1220, 1280, 1300, 1710, 1750, 1920, 2070, 4641, 4660, 5010, 7290, 7330, 8162, 8200, 8350, 8470, 8501, and 8510; the unpleasant pictures were 1120, 1220, 1280, 1300, 1301, 1930, 2120, 3000, 3170, 3530, 3550, 6020, 6540, 6610, 9300, 9440, 9600, and 9911.
Physiological signals were recorded using silver-silver chloride sensors (filled with the appropriate paste) under the left eye (i.e., over the left orbicularis oculi muscle, to measure the blink reflex), on the inside of each arm (to measure the electrocardiogram), above the left brow (i.e., over the corrugator muscle, to measure facial frowning), and on the palm of the hand (to measure skin conductance). A ground sensor was also placed on the right arm. The startle blink reflex was sampled at 1000 Hz for 300 ms following presentation of the acoustic startle probe, filtered (90- to 250-Hz band pass) and integrated (time constant = 123 ms) on-line, and scored off-line for peak magnitude. Corrugator EMG activity (band-pass filter = 90 and 1000 Hz) and skin conductance were sampled at 20 Hz and reduced off-line to change scores (from a 1-s prepicture interval) in half-second bins. The cardiac interbeat interval was measured between consecutive R waves of the electrocardiogram and reduced off-line to heart rate change scores (from a 1-s prepicture baseline) in half-second bins.

Procedure
After the sensors were attached, participants initially viewed a brief series of pictures during an acclimation period. The shock electrode was then placed on the upper arm. Each participant was told that any time a pleasant (or unpleasant, depending on group assignment) picture appeared on the screen, an electric shock could occur through the attached electrode. The participant was also told that when pictures from the other hedonic valence category (i.e., pleasant or unpleasant, depending on group assignment) appeared on the screen, no electric shock could be delivered.

No electric shock was presented during the threat phase. Following this phase of the experiment, each subject underwent a shock workup procedure, in which the intensity of electric shock increased from below threshold until the participant reported the shock was “annoying, but not painful.” Following this procedure, another series of pictures was viewed; these data are not reported here.

Data Analysis
Analyses including gender indicated that it had no main effect and was not involved in any interactions. Therefore, the results reported here are from mixed-model analyses of variance with one between-subjects factor indicating which picture valence cued threat of shock (threat cue: pleasant, unpleasant) and one within-subjects factor indicating the hedonic valence of the viewed picture (picture: pleasant, unpleasant). A significance level of .05 was selected. For skin conductance, one group of participants (threat-pleasant group) tended to show generally larger skin conductance responses than the other group, $F(1, 26) = 3.59, p = .06$. To control for this difference, we standardized skin conductance changes within subjects prior to analysis.

RESULTS
Overall, the startle reflex was potentiated when pictures cued threat of shock, compared with when they cued safety, $F(1, 28) = 11.93, p = .002, \eta^2 = .55$. As Figure 1 illustrates, when cuing threat of shock, pleasant and unpleasant pictures prompted large blinks that were clearly not different in magnitude, $F(1, 28) < 1$. When the pictures cued safety, however, reflex magnitudes were less clearly equivalent, $F(1, 28) = 2.68, p = .11, \eta^2 = .30$. For pleasant pictures, reflex reactions showed large differences depending on whether the pictures cued threat or safety. Reflexes were significantly potentiated when pleasant pictures cued threat of shock, compared with when they cued safety, $F(1, 28) = 4.41, p = .045, \eta^2 = .37$. Comparison with reflexes elicited in the intertrial intervals showed that pleasant pictures that cued shock threat potentiated the startle reflex, $F(1, 15) = 12.41, p = .003, \eta^2 = .47$ (mean intertrial-interval blink = 2.9 µV), whereas pleasant pictures that cued safety did not ($F < 1$, mean intertrial-interval blink = 2.5 µV). For unpleasant pictures, however, there were no differences in reflex magnitude depending on whether the pictures cued threat of shock or safety. Startle magnitude of unpleasant cues was potentiated whether they cued threat of shock or safety, $F < 1$, and, in each case, startle reflexes were facilitated compared with reflexes elicited in the intertrial intervals, $F(1, 13) = 14.87, p = .002, \eta^2 = .73$, and $F(1, 15) = 4.50, p = .05, \eta^2 = .48$, for pictures cuing threat and safety, respectively.

Overall, viewing pictures that cued threat of shock prompted significantly greater heart rate deceleration than viewing pictures that cued safety (see Fig. 2, top panel), $F(1, 26) = 5.20, p = .03, \eta^2 = .14$. Results for heart rate were similar to those for the startle reflex in that both pleasant and unpleasant pictures that cued threat of shock prompted relatively large deceleration, which did not differ between the two categories of pictures, whereas unpleasant pictures prompted greater cardiac deceleration than pleasant pictures when the pictures cued safety, $F(1, 28) = 5.97, p = .02, \eta^2 = .21$. Thus, the difference in heart rate change between threat and safety was significant for pleasant cues, $F(1, 28) = 8.89, p = .006, \eta^2 = .49$, whereas for unpleasant cues, there was no significant difference in the cardiac response as a function of whether the pictures signaled threat or not (see Table 1).

Corrugator EMG (frown) activity was significantly larger when participants viewed pictures under threat, compared with safe, conditions, $F(1, 25) = 4.89, p < .036, \eta^2 = .40$. Although the means listed in Table 1 suggest more corrugator activity during viewing of unpleasant pictures under threat, compared with

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2One participant in the threat-unpleasant group reacted with very high corrugator EMG changes, as evidenced by the relatively high standard error in this condition. When the data for this participant are removed, the mean for unpleasant pictures under threat of shock is 0.37, which is not statistically different from the mean for unpleasant pictures viewed under safe conditions (0.28).
safety, in fact, this difference was not reliable, $F(1, 25) = 1.99, p = .17$. In contrast, the difference in corrugator EMG activity for pleasant pictures viewed under threat versus safety was marginally significant, $F(1, 25) = 3.50, p = .07$, a finding consistent with the hypothesis that pleasant cues that threatened shock were experienced as aversive. A main effect of picture valence, $F(1, 25) = 7.10, p = .01, \eta = .47$, indicated generally larger responses to unpleasant, compared with pleasant, pictures in both the threat and safety conditions.

Changes in skin conductance were larger when participants viewed pictures under threat than when they viewed pictures without shock threat, $F(1, 26) = 11.16, p = .003, \eta = .55$ (see Fig. 2, bottom panel). For both pleasant and unpleasant pictures, pictures associated with threat of shock prompted larger skin conductance changes than pictures viewed free of shock threat, $F(1, 26) = 11.27, p = .002, \eta = .55$, and $F(1, 26) = 11.02, p = .003, \eta = .55$, for pleasant and unpleasant pictures, respectively (see Table 1).

**GENERAL DISCUSSION**

In addition to dramatically potentiating the startle reflex, cues that signaled threat of shock prompted significant cardiac deceleration (fear bradycardia), heightened corrugator EMG (frown) facial displays, and elevated skin conductance activity. This affective profile resembles emotional reactions to aversive visual stimuli, such as pictures of threat, mutilation, and death (e.g., see Bradley et al., 2001; Lang et al., 1993) and supports the hypothesis that startle potentiation when anticipating painful shock is due to defensive activation, rather than to nonspecific anticipatory activity.

A similar pattern of defensive reactivity occurred regardless of whether threat of shock was cued by unpleasant or pleasant pictures. When signaling the possibility of painful electric shock, pleasant and unpleasant pictures prompted large, strikingly parallel response profiles. Most important, reactions to pleasant and unpleasant pictures that cued threat of shock did not differ. When cuing shock threat, pleasant pictures prompted a physiological profile that was consistent with intense defensive activation: potentiated startle reflexes, significant fear bradycardia, heightened corrugator EMG activity, and elevated skin conductance. This is quite different from the pattern of physiological reactivity typically found during perception of pleasant pictures (e.g., Bradley et al., 2001; Lang et al., 1993).
and suggests that previously pleasant cues easily recruit defensive responding on the basis of a simple verbal instruction that shock is possible. Moreover, these data indicate that the prior appetitive association did not inhibit or impede defensive reactions when these cues signaled a new aversive event. From an evolutionary viewpoint, a rapid change from appetitive to aversive association is functional in the natural environment, as an immediate defensive reaction to a cue signaling threat (regardless of its past history) is adaptive.

For unpleasant pictures, defensive reactions were similar regardless of whether these cues signaled threat or safety, and defensive activation did not appear to increase when an unpleasant picture signaled an additional aversive event (e.g., threat of shock). In the case of reflex potentiation, the apparent lack of additivity (i.e., by threat of shock and unpleasant picture valence) is consistent with a hypothesis of saturation in the subcortical structures (e.g., amygdala) that mediate fear-potentiated startle responses (Walker & Davis, 2002). One question concerns whether a ceiling effect obscured increased startle potentiation when subjects viewed unpleasant pictures under shock threat. However, the fact that other defensive reflexes (e.g., cardiac deceleration) were clearly not at a physiological ceiling but showed equivalent responses for pleasant and unpleasant pictures under threat of shock lessens our enthusiasm for this interpretation of the blink data. Moreover, there was no statistical evidence that unpleasant pictures cuing threat of shock prompted larger corrugator EMG responses than pleasant pictures cuing threat of shock. Rather, the EMG data are consistent with the startle-reflex and heart rate data: Pleasant pictures reliably prompted increased corrugator EMG activity under shock threat compared with safety, whereas reactions measured during viewing of unpleasant pictures were equivalent during threat and safety.

When cuing safety, in contrast, unpleasant and pleasant pictures consistently differed, because of the absence of defensive activation for pleasant pictures. Thus, large, consistent differences were found in startle reflexes, facial EMG activity, and cardiac deceleration when comparing pleasant pictures that cued threat and pleasant pictures that cued safety, whereas no differences were found for unpleasant pictures. We obtained a similar pattern in a discriminative human conditioning study in which pleasant (or unpleasant) cues were consistently followed by the presentation (or absence) of electric shock: The difference in reflex magnitude between cues signaling shock or safety was larger for pleasant than for unpleasant pictures (Hamm et al., 1993). In both studies, the main change in reflex modulation was an increase in reflex magnitude when pleasant pictures were associated with a new aversive event.

Taken together, the data are consistent with a defensive-activation hypothesis, according to which cues that signal shock threat activate the defense system, regardless of the cues’ a priori hedonic valence. When cuing safety, unpleasant pictures continue to activate the defense system. That is, their status as nontreat stimuli in this study did not convert unpleasant pictures into appetitive cues. Rather, unpleasant content remained unpleasant and reflexively elicited defensive reactions.

For both pleasant and unpleasant cues, skin conductance activity was elevated when subjects viewed cues that signaled threat of shock, compared with safety. Moreover, the difference in electrodermal reactivity between the threat and safety conditions was the same for pleasant and unpleasant pictures. These data are consistent with the results of previous conditioning studies (cf. Öhman et al., 2000) in which increased skin conductance was found for cues that signaled either aversive (shock) or nonaversive (reaction time task) outcomes. Similarly, skin conductance changes when observers view pleasant or unpleasant pictures (relative to neutral pictures) are large and equivalent (Lang et al., 1993). Thus, rather than simply indexing defensive activation, the sympathetically mediated skin conductance response may more broadly reflect the signal properties of the cuing stimulus.

In summary, anticipating the presentation of a potentially painful (but not yet experienced) electric shock prompted somatic and autonomic reflexes consistent with activation of the defensive system. These effects were evident regardless of whether the signaling cues were pleasant or unpleasant pictures. When these same pleasant and unpleasant pictures were safe, however, they showed their normal, intrinsic response profiles—defensive or appetitive—suggesting that the experimental procedure involved no new affective learning for these cues. The similarity in physiological reactions to physical threat and to pictures experienced as affectively unpleasant indicates

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### TABLE 1

Means for the Physiological Measures During Viewing of Pleasant or Unpleasant Pictures That Cued Threat of Shock or Were Free of Shock Threat

<table>
<thead>
<tr>
<th>Cue</th>
<th>Heart rate change</th>
<th>Corrugator change</th>
<th>Skin conductance</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Threat</td>
<td>Safety</td>
<td>Difference</td>
</tr>
<tr>
<td>Pleasant</td>
<td>−2.6 (0.97)</td>
<td>1.1 (0.69)</td>
<td>−3.7</td>
</tr>
<tr>
<td>Unpleasant</td>
<td>−1.8 (0.74)</td>
<td>−1.2 (0.63)</td>
<td>−0.6</td>
</tr>
<tr>
<td>Overall</td>
<td>−2.2 (0.62)</td>
<td>−0.14 (0.51)</td>
<td>−2.1</td>
</tr>
</tbody>
</table>

Note. Standard errors are in parentheses. Heart rate change is reported in beats per minute, corrugator electromyographic change in microvolts, and skin conductance change in standardized units.
that emotional reactions to media and to real-world threats (or attractions) have a common motivational foundation. Whether these parallel psychophysiological events actually involve common brain structures and circuits (e.g., see Funayama, Grillon, Davis, & Phelps, 2001) will be determined by the outcome of future research.

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REFERENCES


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