Emotion

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Fear learning can be adaptively advantageous, but only if the learning is integrated with higher-order cognitive processes that impact goal-directed behaviors. Recent work has demonstrated generalization (i.e., transfer) of conditioned fear across perceptual dimensions and conceptual categories, but it is not clear how fear generalization influences other cognitive processes. The current study investigated how associative fear learning impacts higher-order visuospatial attention, specifically in terms of attentional bias toward generalized threats (i.e., the heightened assessment of potentially dangerous stimuli). We combined discriminative fear conditioning of color stimuli with a subsequent visual search task, in which targets and distractors were presented inside colored circles that varied in perceptual similarity to the fear-conditioned color. Skin conductance responses validated the fear-conditioning manipulation. Search response times indicated that attention was preferentially deployed not just to the specific fear-conditioned color, but also to similar colors that were never paired with the aversive shock. Furthermore, this attentional bias decreased continuously and symmetrically from the fear-conditioned value along the color spectrum, indicating a generalization gradient based on perceptual similarity. These results support functional accounts of fear learning that promote broad, defensive generalization of attentional bias toward threat.

Keywords: emotion, anxiety, fear generalization, visual attention, attentional bias

The transfer of learning is an evolutionarily important phenomenon. To make predictions about the future, organisms need to be able to generalize learned information to new situations. This capacity is particularly critical in fear learning; for example, an aversive experience with a single vicious dog might teach a child to be wary of all dogs. Although the generalization of fear learning is a key construct in theories of animal behavior (e.g., aposematic warning coloration; Gamberale-Stille & Tullberg, 1999), research has just begun to systematically explore fear generalization mechanisms in humans (see Dunsmoor & Murphy, 2015; Dymond, Dunsmoor, Vervliet, Roche, & Hermans, 2015). Human fear generalization studies typically use classical fear conditioning to imbue a neutral stimulus (conditioned stimulus; CS) with an aversive meaning by placing it in a predictive relationship with an electrical shock (unconditioned stimulus; US). Fear responses—as quantified by increases in skin conductance response (SCR), fear-potentiated startle reflex, or subjective perceived likelihood of shock—are then compared across a continuum of stimuli that vary in perceptual or conceptual similarity to the CS, revealing a generalization gradient of fear responses to the unreinforced stimuli (e.g., Dunsmoor, White, & LaBar, 2011; Lissek et al., 2008). The graded nature of fear generalization is attributed to many factors—from learned discrimination (Dunsmoor & LaBar, 2013) to perceived threat intensity (Dunsmoor, Mitroff, & LaBar, 2009)—and may reflect an adaptive balance of when to transfer fear learning (see Dunsmoor & Paz, 2015).

Although fear generalization in humans has been demonstrated with basic behavioral and physiological measures, it is not known how fear generalization processes impact higher-order cognitive functions. In one study, fear generalization emerged in a decision-making task, such that participants avoided decision pathways associated with unreinforced stimuli that were perceptually similar to a CS (van Meurs, Wiggert, Wicker, & Lissek, 2014). However, the effects of fear learning on the specificity of perceptual decisions are less clear. Although some studies show that aversive reinforcement impairs discrimination of the CS (i.e., widens generalization curves; Resnik, Sobel, & Paz, 2011; Schechtman, Laufer, & Paz, 2010), other studies find that aversive learning actually enhances discrimination (Åhs, Miller, Gordon, & Lundström, 2013; Li, Howard, Parrish, & Gottfried, 2008; Lim & Pessoa, 2008). These discrepant results have been theorized to reflect two complementary aspects of fear learning: coarse generalization for faster defensive behaviors (i.e., reacting to similar items that might also be threatening) and finer discrimination of the specific CS features for enhanced threat identification (Åhs et

al., 2013; Resnik et al., 2011; see also McTeague, Gruss, & Keil, 2015).

Given that one functional consequence of fear activation is to promote vigilance toward other possible threats in the environment, it is important to determine whether or not fear learning induces generalization in the allocation of visuospatial attention. Threatening stimuli, including fear-conditioned stimuli (Smith, Most, Newsome, & Zald, 2006), tend to elicit rapid attentional orienting and prolonged attentional disengagement (see Vuilleumier, 2005). Attentional prioritization of threat is thought to be evolutionarily adaptive because it prepares the system to respond optimally (Öhman, 2009) and may even maintain fear and anxiety to flexibly elicit appropriate behavioral responses (Van Bockstaele et al., 2014). Prior studies have also shown that in visual search tasks (i.e., finding a target among distractors), fear-conditioned stimuli capture visual attention, even when they are irrelevant or disadvantageous for task performance (e.g., Notebaert, Crombez, Van Damme, DeHouwer, & Theeuwes, 2011; Schmidt, Belopolsky, & Theeuwes, 2015), indicating a relatively automatic influence of threat detection on goal-directed behavior.

However, an important question remains: How specific or how generalizable is attentional bias toward threat? Although much research has examined how fear associations impact visuospatial attention, no prior study has examined whether fear-conditioned attentional biases generalize across perceptual similarity. Furthermore, the divergent effects of fear learning on perceptual discrimination (e.g., Li et al., 2008; Resnik et al., 2011) make it unclear whether fear generalization would manifest in related goal-directed behaviors. Visuospatial attention (i.e., the selection of information to be processed) is obviously closely linked to perception (i.e., the processing of sensory stimuli), with behavioral and neural evidence showing that different patterns of attention change what we perceive (e.g., Carrasco, Ling, & Read, 2004). Reciprocally, the extent of perceptual discrimination also plays an important role in attention, such that local stimulus contrast feeds into calculations of attentional priority (e.g., Theeuwes, 2010). Thus, if aversive reinforcement increases finer tuned sensitivity to (i.e., more accurate identification of) a CS, then attentional bias should be limited to the specific stimulus, enhancing the detection of a specific threat. On the other hand, if fear conditioning triggers broad and rapid defensive learning mechanisms, then attentional biasing behaviors should generalize across similar stimuli for swift detection of many potential threats. Consistent with the latter mechanistic perspective, we hypothesized that fear generalization gradients would manifest in visuospatial attention—even in task-irrelevant circumstances—such that the degree to which attention was biased to unreinforced stimuli would vary continuously with their perceptual similarity to the CS. This predicted result would importantly extend recent efforts in identifying neurobehavioral correlates of fear generalization to show how generalization mechanisms interact with higher-order cognitive processes to impact goal-directed behavior.

Method

Participants

Forty Duke University undergraduate students (10 male; average age 19 years, $SD = 1.35$; 50% Asian, 45% White, 5% Black;

97.5% non-Hispanic) participated in the study for course credit, and all signed informed consent in accordance with Duke University's Institutional Review Board. All had normal or normal-to-corrected vision and were screened for clinical levels of trait anxiety and depression before participating (see *Self-report instruments*). Data from an additional 11 participants were excluded for poor overall search performance: 1 for low accuracy (<80%) and 10 for not responding to more than 20% of visual search trials. It is possible that the longer, multiple-phase setup before the visual search task (i.e., self-report questionnaires, fear conditioning protocol) contributed to the large number of participants who failed to follow task instructions.

Apparatus

All phases of the experiment were conducted on a Windows Optiplex 755 computer, running Windows 7, and were programmed in Matlab using the Psychophysics Toolbox, Version 3.0 (Brainard, 1997). Participants viewed experimental displays on a 19-in. liquid crystal display monitor with a refresh rate of 60 Hz and screen resolution of 1,280 × 1,024 pixels at an approximate distance of 60 cm. Psychophysiological recordings and electrical shocks were administered with the MP-150 BIOPAC system (BIOPAC Systems, Goleta, CA).

Stimuli

Fear conditioning. As in Dunsmoor and LaBar (2013), participants learned to discriminate between a reinforced (CS+) color and a nonreinforced (CS–) color from a continuous spectrum of equiluminant color values. The five color values of interest (spectral wavelength values of 489, 493, 494, 496, and 500 nm) had been previously piloted to span incrementally from subjectively perceived "blue" to "green" and to be discriminable from one another (Dunsmoor & LaBar, 2013) for the same general population sampled here using the same experimental apparatus. The value used for the CS+ (494 nm) was nearest the point of subjective equality between blue and green. The value used for the CS– was one of the two endpoints, such that in Group 1, 19 subjects had a blue (489 nm) CS– and in Group 2 21 subjects had a green (500 nm) CS–; CS– group membership did not affect any key analyses; thus, data have been collapsed across groups. Color values were presented as colored circles (diameter = 3.8°, stroke width = 0.2°) on a white background. The aversive US was a 6-ms electrical shock administered to the palmar surface of the right wrist; the intensity of the shock was individually determined using an ascending staircase procedure to reach a level that was "highly annoying, but not painful" (Dunsmoor et al., 2009).

Visual search. Search stimuli were compound stimuli, consisting of a black line (extending 2.2°, stroke width = 0.2°) in the center of a colored circle (diameter = 3.8°, stroke width = 0.2°). Lines were presented horizontally, vertically, or tilted 45° to either side of the horizontal or vertical plane. On each trial, the search array consisted of five stimuli, equally spaced on an imaginary circle with a radius of 8° visual angle. Only one of the stimuli could be the target, containing either a horizontal or a vertical line; the remaining stimuli contained tilted line distractors. Circle colors were drawn from the five blue-green values of interest or pseudo-randomly chosen from colors beyond the range of blue-green

discrimination values (e.g., red or yellow). Within each array, colors were jittered across color space to avoid multiple similar colors in an array. Luminance of the blue-green colors fell within the range of luminance values of non-blue–green colors. Visual search stimuli and procedures were adapted from similar previous studies (e.g., Notebaert et al., 2011; Theeuwes, 1991).

Self-report instruments. Trait anxiety was assessed with the State–Trait Anxiety Inventory (STAI-T; Spielberger, Gorsuch, Lushene, Vagg, & Jacobs, 1983), a 20-item questionnaire that measures anxiety in adults. Trait anxiety was overall low, limited in range ($M = 33.5$, $SD = 7.2$), and not associated with any key findings; therefore, it will not be discussed further. Depression was assessed with the Quick Inventory of Depressive Symptomatology (QIDS-SR; Rush et al., 2003), a 16-item questionnaire that measures depressive symptoms in adults to exclude high-scoring individuals from the fear-conditioning paradigm; however, no participants ($M = 3.4$, $SD = 2.6$) met the exclusionary criterion.

Procedure

The session began with participants completing the STAI-T and QIDS-SR, followed by calibration of each individual's tolerance level to the electrical shock. The rest of the experiment consisted of four phases in the following order: baseline, fear conditioning, visual search, and identification (see Figure 1).

Baseline. The baseline phase allowed for preexposure measures of arousal and included five trials of each blue-green color value (25 total). Each trial began with a central fixation cross for 500 ms; followed by an array of five empty circles for 4 s; with intertrial periods of 4, 5, or 6 s (Figure 1A). Only one of the five circles was colored; the remaining circles were the same shade of gray. The circles were equally spaced on an imaginary circle with a radius of 8° visual angle, and the location of the colored circle randomly varied.
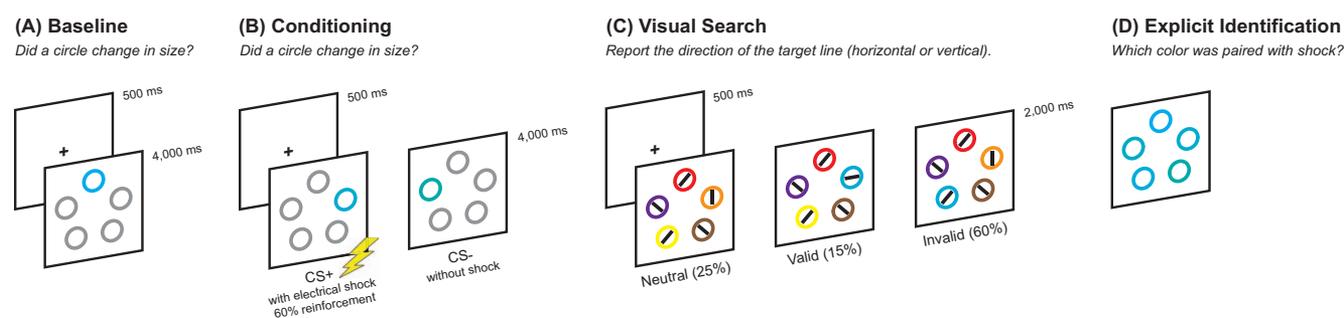
Baseline stimuli were presented within the context of a vigilance task, in which participants were instructed to report via keypress

when any of the circles changed in size. On 10 of 25 trials, one circle increased in size by 8% for 100 ms and then returned to original size. The vigilance task ensured that participants were paying attention to the visual stimuli.

Fear conditioning. The conditioning phase also used the vigilance task setup to present 10 CS+ trials and 10 CS– trials (20 total) with pseudorandomized intertrial intervals of 7, 8, or 9 s (Figure 1B). In 6 of the 10 trials (pseudorandomly determined), US delivery coterminated with the visual termination of the CS+ (delay conditioning). The CS– was an explicitly nonreinforced control and was never paired with the US. The order of CS+ and CS– trials was pseudorandomized across subjects. Before the conditioning phase, participants were explicitly told that electrical stimulation would always be paired with only one of the two colors but were not informed which color was the CS+.

Visual search. In the visual search task, each trial began with a central fixation cross for 500 ms. Then a search array of five compound stimuli was presented for 2,000 ms (Figure 1C). Participants were instructed to identify the target as quickly as possible, reporting via keypress whether the target line was horizontal or vertical. The visual search phase consisted of a practice block of 20 trials and five experimental blocks of 100 (+4) trials each, with a short break after each block. Half of the trials contained a horizontal target and the other half a vertical target.

Trials were classified across two factors: validity (valid, invalid, neutral) and blue-green color value. Validity conditions were determined by whether a blue-green color value matched the location of the search target (valid; 15%), a search distractor (invalid; 60%), or did not appear in the search array at all (neutral; 25%). Note that the appearance of a blue-green color value in the search display was technically orthogonal and unrelated to the search task. The frequencies of valid and invalid trials were distributed equally across all five blue-green color values, and all trial types were mixed within blocks. To ensure that the CS+ remained threatening, participants were told that some trials would contain

(A) Baseline
Did a circle change in size?

(B) Conditioning
Did a circle change in size?

(C) Visual Search
Report the direction of the target line (horizontal or vertical).

(D) Explicit Identification
Which color was paired with shock?

Figure 1. Trial sequences for the four experimental phases. (A) The baseline phase presented the five blue-green colors of interest (i.e., spectral wavelength values of 489, 493, 494, 496, and 500 nm) within the context of a vigilance task, in which participants reported when any circle changed in size. Blue-green colors were presented individually within an array of gray circles to allow for preexposure measures of arousal. No electrical shocks occurred during this phase. (B) The conditioning phase also used the same vigilance task to present only the reinforced color (CS+) and nonreinforced color (CS–); the CS+ was paired with an electrical shock at a reinforcement rate of 60%. (C) During the visual search task, participants reported the direction of the target line (horizontal or vertical). A blue-green color of interest appeared around the location of a target (valid; 15%), the location of a distractor (invalid; 60%), or not at all (neutral; 25%). (D) After the search task, participants explicitly identified which of the five blue-green colors were originally paired with shock during the conditioning phase. See the online article for the color version of this figure.

electrical shocks. Although the CS+ was no longer reinforced at a rate of 60%, the CS+ was randomly reinforced by the US four times in each experimental block (i.e., 100 + 4 total trials per block). The reinforced CS+ always appeared around a distractor (i.e., invalid), and these trials were not included in subsequent analyses.

Explicit identification. After the search task, participants were given a forced-choice display of the five blue-green color values and asked to explicitly identify which value had been paired with the shock (Figure 1D). This retrospective identification task permits an assessment of fear generalization in memory representations of the CS (Dunsmoor & LaBar, 2013).

SCRs. SCRs were recorded during baseline and conditioning phases of the experiment from the middle phalanx of the second and third digits of the left hand. Using AcqKnowledge software (BIOPAC Systems), an SCR was considered related to stimulus presentation if the trough-to-peak response occurred 1–4 s after stimulus onset, lasted between 0.5 and 5.0 s, and was greater than 0.02 mS in amplitude. A response that did not meet these criteria was scored as zero. Raw SCR scores were normalized by range correction using each participant's maximum SCR, and range-corrected values were square-root–transformed to normalize the distribution. Two participants were characterized as "nonresponders" based on a lack of measurable SCR and were removed from SCR analysis (LaBar, Cook, Torpey, & Welsh-Bohmer, 2004).

Results

Baseline and Conditioning

Data for all analyses were collapsed across CS– color group (i.e., whether the explicitly nonreinforced stimulus was blue or green). For the baseline phase, SCR data were analyzed by repeated-measures analysis of variance (ANOVA) across color (five blue-green values). As expected, baseline SCRs were low, with no effect of color, $F(4, 148) = 0.93$, $p = .446$, $\eta_p^2 = .03$ (Figure 2A). To assess successful acquisition of conditioned fear to the CS+, we compared SCRs for just the intermediate CS+ value versus the endpoint CS– value across baseline and conditioning phases (see Table 1). A two-way repeated-measures ANOVA yielded significant main effects of both phase, $F(1, 37) = 7.75$, $p = .008$, $\eta_p^2 = .17$, and color, $F(1, 37) = 11.79$, $p = .001$, $\eta_p^2 = .24$; however, there was also a significant interaction effect, $F(1, 37) = 19.76$, $p < .001$, $\eta_p^2 = .35$, indicating that the magnitude of differential SCR varied by phase (Figure 2A). Post hoc paired t tests within phase revealed no baseline difference between the CS– and CS+ values but a significant difference during conditioning, $t(37) = 5.86$, $p < .001$, $d = 0.95$. Likewise, paired t tests within color revealed only a significant increase in SCR for the CS+ value, $t(37) = 5.05$, $p < .001$, $d = 0.82$. Thus, participants demonstrated successful acquisition of conditioned fear to only the CS+ value.

Visual Search

Validity effects. Our primary measure of interest was response time (RT) for correct visual search trials (see Table 2). To replicate the finding that visual attention is biased toward fear-associated stimuli (Notebaert et al., 2011), we first analyzed RTs for only trials that contained the specific CS+ color value (i.e., valid-CS+ and invalid-CS+) as well as neutral trials. A repeated-measures ANOVA revealed a main effect of search validity, $F(2, 78) = 28.2$, $p < .001$, $\eta_p^2 = .42$ (Figure 2C). Planned contrasts showed that participants were faster to respond when the CS+ coincided with the location of the target, $t(39) = 4.47$, $p < .001$, $d = 0.71$, and slower when the CS+ coincided with the location of a distractor, $t(39) = 3.12$, $p = .004$, $d = 0.49$, compared with a neutral baseline.

To ensure that search validity effects were not due to a speed/accuracy tradeoff, we also analyzed search accuracy rates (see Table 2). A repeated-measures ANOVA revealed no significant differences across validity conditions, either for the specific CS+ color value, $F(2, 102) = 0.90$, $p = .408$, $\eta_p^2 = .02$, or across all colors, $F(2, 102) = 0.43$, $p = .649$, $\eta_p^2 = .01$. Thus, validity effects could not be attributed to a speed/accuracy tradeoff during the search.

Generalization. To examine the presence of fear generalization gradients in attention, search RTs were analyzed with a repeated-measures ANOVA across validity (valid, invalid) and color (five blue-green values; Figure 2B). A perceptually based fear generalization gradient would manifest as a quadratic trend across the interaction effect, which indeed was found, $F(1, 39) = 6.43$, $p = .015$, $\eta_p^2 = .14$. There was also a significant main effect of validity, $F(1, 156) = 62.7$, $p < .001$, $\eta_p^2 = .62$, but both the main effect of color and the interaction between validity and color were nonsignificant ($ps > .25$). In other words, all five colors demonstrated significant attentional biases, to varying extents. In line with previous findings of fear generalization in SCRs across these same color stimuli (Dunsmoor & LaBar, 2013), we hypothesized that attentional bias (i.e., validity effects) to the CS+ would be significantly greater than to the CS–. Indeed, comparing just the CS+ and CS– colors, a repeated-measures ANOVA across validity (valid, invalid) and color (CS+, CS–) revealed a significant interaction effect, $F(1, 39) = 5.39$, $p = .026$, $\eta_p^2 = .12$.

To better assess fear generalization gradients in attentional bias across the tested color range, we calculated a singular measure of attentional bias for each individual: (invalid RT – valid RT)/ (neutral RT). This normalized difference score reflects the absolute RT difference as a proportion of neutral RT, such that positive values indicate greater attentional bias (see Dowd, Kiyonaga, Egner, & Mitroff, 2015). A repeated-measures ANOVA again revealed a significant quadratic trend, $F(1, 39) = 5.37$, $p = .026$, $\eta_p^2 = .12$, indicating a continuous and graded inverse U-shaped curve in attentional bias (Figure 2D). The effect of color was nonsignificant, $F(4, 156) = 1.08$, $p = .372$, $\eta_p^2 = .03$. As previously discussed, we hypothesized that attentional bias would be greater to the CS+ compared with the CS–; a post hoc one-tailed paired t test revealed significantly higher attentional bias for the CS+ value (494 nm for both groups), $t(39) = 1.86$, $p = .035$, $d = 0.29$, compared with the CS– value. Furthermore, attentional bias to the value adjacent to the CS+ but further away from the CS– (496 nm for Group 1, 493 nm for Group 2) was also significantly higher than to the CS– value, $t(39) = 1.71$, $p = .047$, $d = 0.27$. These two values were not significantly different from each other, $p > .4$.

Normalized difference scores were also analyzed with a two-way repeated-measures ANOVA across side (to the left of the
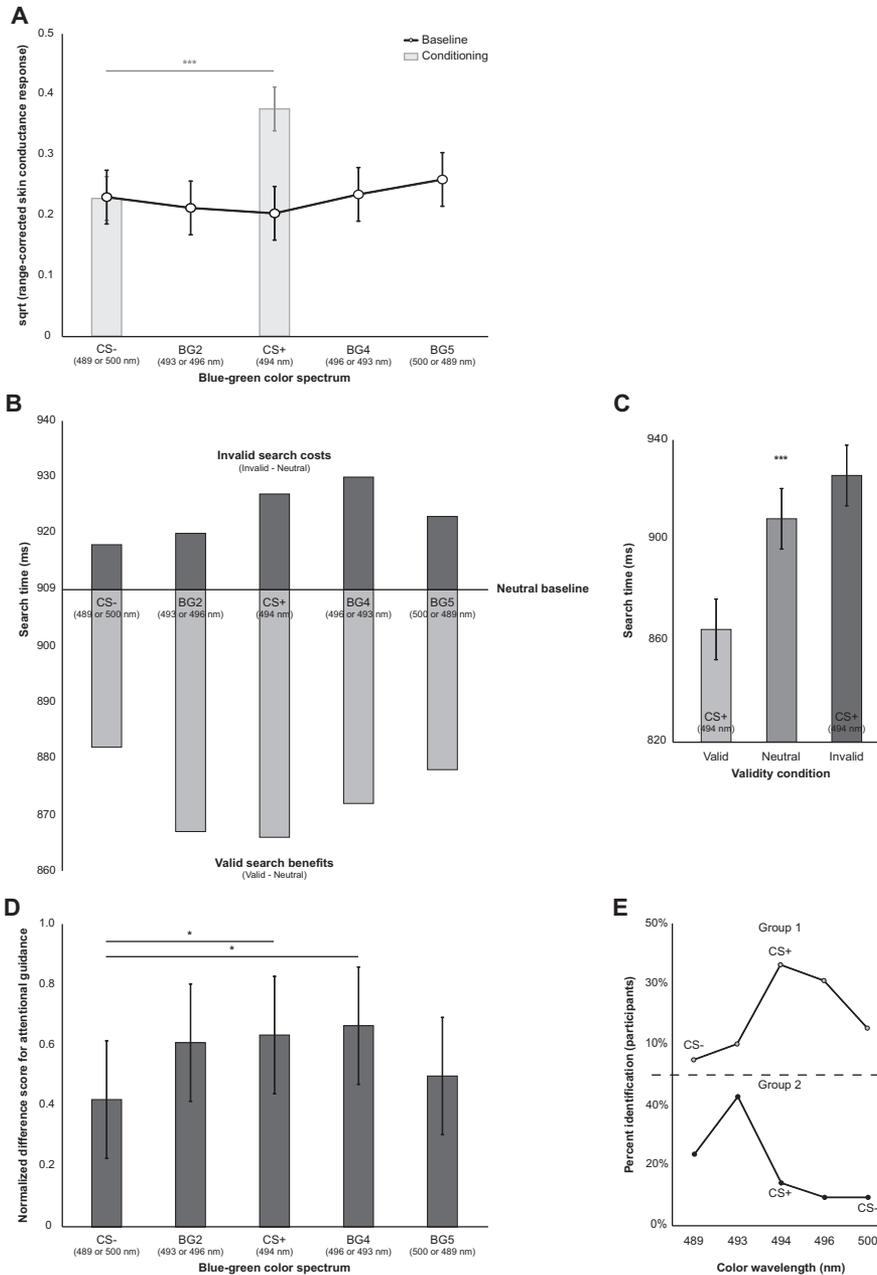
Figure 2. Behavioral results indicate successful conditioning and subsequent generalization across similar percepts in visual attention and explicit identification. (A) SCRs were low and undifferentiated across the blue-green color spectrum during the baseline phase (white circles) but were significantly greater for the reinforced CS (CS+) vs. unreinforced CS (CS–; light gray bars), indicating successful conditioning. (B) Search times during the visual search task revealed significant effects of validity across blue-green colors such that participants were faster when a blue-green color matched the location of a target (valid; light gray) and slower when a blue-green color matched the location of a distractor (invalid; dark gray) compared with trials in which no blue-green color reappeared (neutral baseline). (C) Search times for just the CS+ color revealed significant effects of validity. (D) Search validity effects were recalculated into a single normalized difference score that reflects the degree of attentional guidance. Across the blue-green color spectrum, there was a significant quadratic trend, supporting generalization based on perceptual similarity in attentional bias. Attentional bias was significantly lower for the CS– color compared with the CS+ color and an unreinforced blue-green color farther away from the CS–. (E) When asked to identify which stimulus was the CS+ at the end of the experiment, 47% of participants in Group 1 (gray circles) mistakenly identified a stimulus that was more green than the actual CS+, and 67% of participants in Group 2 (black circles) mistakenly identified a stimulus that was more blue than the actual CS+. Error bars represent 95% confidence interval. $^* p < .05$; $^{***} p < .001$.

Table 1
Mean SCRs

Phase	Explicitly nonreinforced color (CS−)	Reinforced color (CS+)
Baseline	.230 (.17)	.203 (.18)
Conditioning	.228 (.20)	.376 (.18)

Note. Standard deviations are presented in parentheses.

CS+ or to the right of the CS+ along the color spectrum) and distance (how far away from the CS+ in color hue). There was a significant main effect of distance, $F(1, 39) = 4.56$, $p = .039$, $\eta_p^2 = .11$, but no significant effects of side or the interaction, $ps > .5$. This result indicates that attentional bias effects dropped off from the CS+ in a symmetrical fashion, centered at the CS+ value, consistent with a Gaussian-shaped fear generalization function based on perceptual similarity (Dunsmoor & LaBar, 2013).

Retrospective CS+ identification. After completing the visual search task, only 10 of 40 participants correctly identified the 494-nm stimulus as the CS+ whereas 15 participants mistakenly identified an unreinforced value opposite the CS− along the color spectrum (the greener 496-nm stimulus for Group 1 and the bluer 493-nm stimulus for Group 2) as the CS+. Furthermore, eight participants mistakenly identified the unreinforced color endpoint opposite the CS− stimulus (500 nm for Group 1 and 489 nm for Group 2) as the CS+. Across both groups, a χ^2 test revealed that stimulus color significantly affected CS+ identification ratings compared with chance, $\chi^2(4) = 11.75$, $p = .019$ (Figure 2E). We also examined whether retrospective identification accuracy of the CS+ was a reflection of initial learning, as indexed by differential SCRs (CS+ > CS−), but we found no difference between accurate and inaccurate subgroups, $t(17) = 0.04$, $p = .968$, $d = .01$. Moreover, retrospective identification accuracy was unrelated to validity effects during visual search (all validity × identification accuracy $ps > .15$).

Discussion

The present study used discriminative fear conditioning and a subsequent visual search task to demonstrate, for the first time, that generalization of fear across similar percepts manifests in visuospatial attention. Specifically, attention was preferentially deployed not just to the specific fear-conditioned color but also to other perceptually similar colors that were never paired with the aversive US on a visual search task in which the color of the fear-conditioned stimulus was task irrelevant. Although previous studies have demonstrated fear generalization gradients in autonomic responses (e.g., Dunsmoor & LaBar, 2013), the current results provide new evidence for effects of fear generalization on higher-order visual cognition.

After successful conditioning of the CS+ color, participants exhibited canonical search validity effects for the CS+ color (i.e., faster responses when the CS+ matched the target and slower responses when the CS+ matched a distractor), replicating the attentional prioritization of threat found by Notebaert and colleagues (2011). These search validity effects were significant across the five blue-green colors, even the explicitly nonreinforced CS−, likely because of high perceptual similarity across a limited

range of color values. Thus, it is striking that there was a differential gradient of attentional bias from the CS+ to other perceptually similar colors. This gradient followed a significant quadratic trend, such that validity effects decreased continuously and symmetrically from the reinforced CS+ value along the color spectrum. This pattern is indicative of a fear generalization gradient based on perceptual similarity (Dunsmoor & LaBar, 2013).

It is interesting to note that most participants mistakenly identified an unreinforced color further away from the CS− as the color that had been paired with shock, suggesting a generalization-induced bias in the retrospective memory for the fear association, consistent with our prior work (Dunsmoor & LaBar, 2013). However, in contrast to Dunsmoor and LaBar's (2013) paradigm, our generalization test featured several blocks of a visually demanding search task in which CS− and CS+ colors were repeatedly presented as irrelevant, distractor stimuli, likely leading to fear extinction (even with occasional reinforcement of the CS+). Prolonged fear extinction could have diminished the robustness of fear generalization in attentional bias, and the current identification results may not be a pure reflection of a generalization-induced memory bias.

The current results support the idea that fear generalization across similar percepts, which has been previously demonstrated in autonomic responses (Dunsmoor & LaBar, 2013), can manifest in higher cognitive behaviors, such as attention and perhaps even memory. Previous studies using auditory and olfactory stimuli have found contradictory effects of fear learning on perceptual discrimination, leading to divergent hypotheses about whether aversive reinforcement enhances discrimination through a slower, cortical system or generalizes via a fast, defensive subcortical system (i.e., the amygdala; Resnik et al., 2011). The present findings of fear generalization in visual attention are compatible with the latter hypothesis because attentional prioritization of threat is thought to support a rapid, defensive preparedness via interactions between the amygdala and frontoparietal attentional networks (Öhman, 2009; Vuilleumier, 2005). Even so, a broad and rapid fear learning mechanism must be limited along some dimension of threat relevance (or threat uncertainty; Onat & Büchel,

Table 2
Mean RT and Accuracy for Visual Search Task for Each Trial Type

Color	Neutral	Valid	Invalid
RT (ms)			
No blue-green	909 (158)		
BG1 (CS−)		881 (158)	917 (180)
BG2		866 (155)	919 (171)
BG3 (CS+)		865 (164)	926 (144)
BG4		871 (164)	929 (173)
BG5		877 (167)	922 (172)
Accuracy (%)			
No blue-green	86.6 (14.7)		
BG1 (CS−)		86.5 (16.8)	86.3 (14.8)
BG2		86.3 (15.4)	87.6 (14.0)
BG3 (CS+)		87.7 (16.4)	86.8 (14.2)
BG4		87.8 (15.3)	86.8 (15.5)
BG5		86.8 (17.0)	87.3 (15.1)

Note. Standard deviations are presented in parentheses.

2015) so as to avoid the maladaptive overgeneralization of fear associations (see Dunsmoor & Paz, 2015).

Attentional bias in the current paradigm was unlikely to be driven by a slower, top-down strategy of using threat-related colors to find the target—although blue-green colors did infrequently coincide with the target location (15% valid), most trials featured blue-green colors appearing around a distractor (60% invalid), such that strategically attending to blue-green colors would actually be detrimental for the search task (also see Notebaert et al., 2011). Such involuntary attentional effects may themselves perpetuate fear generalization in a feedback manner—unintentional attentional capture operates on perceptual (Becker, Folk, & Remington, 2010) and conceptual (Wyble, Folk, & Potter, 2013) relational properties, even without aversive associations, and this spread of attentional bias across perceptually or conceptually similar items could drive further generalization along the same dimensions.

The demonstration of fear generalization gradients in visual attention may have implications for clinical models of anxiety because anxiety disorders are characterized by impairments at several stages of threat processing: overgeneralization of fear associations (see reviews by Dunsmoor & Paz, 2015; Dymond et al., 2015), enhanced perception of threat (see Clark, 1999), and exaggerated attentional bias toward threat (see Bar-Haim, Lamy, Pergamin, Bakermans-Kranenburg, & van IJzendoorn, 2007). Although our current sample did not exhibit clinical levels of trait anxiety, overgeneralization of fear in anxious populations could potentially manifest as amplified attentional bias toward stimuli that were never associated with threat in the first place. Furthermore, certain anxiety disorders exhibit memory biases for threatening information, which may further potentiate anxiety (Mathews & MacLeod, 2005). Thus, the consequences of fear learning and generalization on attention and long-term memory may be part of a greater maladaptive feedback loop.

The effects of fear conditioning bear striking similarities to the effects of reward associations on visuospatial attention (for review, see Anderson, 2015a)—reward-associated stimuli are preferentially attended even when the rewarding feature is task irrelevant and when the motivational salience of reward is no longer applicable (e.g., Le Pelley, Pearson, Griffiths, & Beesley, 2015). Although there has been divergent evidence for the transfer of reward-induced attentional bias (e.g., Anderson, 2015b (Psychonomic Bulletin & Review) vs. Anderson, Laurent, & Yantis, 2012), two recent studies found that the impact of reward on nonspatial visual attention did generalize across scene semantics and object categories, such that novel exemplars of a previously rewarded category of visual scenes or objects also captured attention (Failing & Theeuwes, 2015; Hickey, Kaiser, & Peelen, 2015). Although the influence of reward on visuospatial attention has not been explicitly examined across continuous spectrums of perceptual or conceptual similarity, a parallel "reward generalization gradient" in attentional bias could reflect a more general mechanism for how the learning of any predictive associations impacts higher-order cognitive behavior (also see Le Pelley, 2010).

By combining discriminative fear conditioning with a subsequent visual search task, the present study supports theoretical ideas regarding a broad, defensive generalization of attentional bias toward threat. Although much of the literature to date has focused on the cognitive and neural mechanisms by which learning

spreads (e.g., Dunsmoor & Murphy, 2015), these findings emphasize the behavioral consequences of fear generalization. Further research into the interaction between maladaptive overgeneralization and exaggerated attentional bias may provide new insights into the development and treatment of particular anxiety disorders.

References

Åhs, F., Miller, S. S., Gordon, A. R., & Lundström, J. N. (2013). Aversive learning increases sensory detection sensitivity. *Biological Psychology, 92,* 135–141. http://dx.doi.org/10.1016/j.biopsycho.2012.11.004

Anderson, B. A. (2015a). The attention habit: How reward learning shapes attentional selection. *Annals of the New York Academy of Sciences.* Advanced online publication. http://dx.doi.org/10.1111/nyas.12957

Anderson, B. A. (2015b). Value-driven attentional priority is context specific. *Psychonomic Bulletin & Review, 22,* 750–756. http://dx.doi.org/10.3758/s13423-014-0724-0

Anderson, B. A., Laurent, P. A., & Yantis, S. (2012). Generalization of value-based attentional priority. *Visual Cognition, 20,* 647–658. http://dx.doi.org/10.1080/13506285.2012.679711

Bar-Haim, Y., Lamy, D., Pergamin, L., Bakermans-Kranenburg, M. J., & van IJzendoorn, M. H. (2007). Threat-related attentional bias in anxious and nonanxious individuals: A meta-analytic study. *Psychological Bulletin, 133,* 1–24. http://dx.doi.org/10.1037/0033-2909.133.1.1

Becker, S. I., Folk, C. L., & Remington, R. W. (2010). The role of relational information in contingent capture. *Journal of Experimental Psychology: Human Perception and Performance, 36,* 1460–1476. http://dx.doi.org/10.1037/a0020370

Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision, 10,* 433–436. http://dx.doi.org/10.1163/156856897X00357

Carrasco, M., Ling, S., & Read, S. (2004). Attention alters appearance. *Nature Neuroscience, 7,* 308–313. http://dx.doi.org/10.1038/nn1194

Clark, D. M. (1999). Anxiety disorders: Why they persist and how to treat them. *Behaviour Research and Therapy, 37*(Suppl. 1), S5–S27. http://dx.doi.org/10.1016/S0005-7967(99)00048-0

Dowd, E. W., Kiyonaga, A., Egner, T., & Mitroff, S. R. (2015). Attentional guidance by working memory differs by paradigm: An individual-differences approach. *Attention, Perception, & Psychophysics, 77,* 704–712. http://dx.doi.org/10.3758/s13414-015-0847-z

Dunsmoor, J. E., & LaBar, K. S. (2013). Effects of discrimination training on fear generalization gradients and perceptual classification in humans. *Behavioral Neuroscience, 127,* 350–356. http://dx.doi.org/10.1037/a0031933

Dunsmoor, J. E., Mitroff, S. R., & LaBar, K. S. (2009). Generalization of conditioned fear along a dimension of increasing fear intensity. *Learning & Memory, 16,* 460–469. http://dx.doi.org/10.1101/lm.1431609

Dunsmoor, J. E., & Murphy, G. L. (2015). Categories, concepts, and conditioning: How humans generalize fear. *Trends in Cognitive Sciences, 19,* 73–77. http://dx.doi.org/10.1016/j.tics.2014.12.003

Dunsmoor, J. E., & Paz, R. (2015). Fear generalization and anxiety: Behavioral and neural mechanisms. *Biological Psychiatry, 78,* 336–343. http://dx.doi.org/10.1016/j.biopsych.2015.04.010

Dunsmoor, J. E., White, A. J., & LaBar, K. S. (2011). Conceptual similarity promotes generalization of higher order fear learning. *Learning & Memory, 18,* 156–160. http://dx.doi.org/10.1101/lm.2016411

Dymond, S., Dunsmoor, J. E., Vervliet, B., Roche, B., & Hermans, D. (2015). Fear generalization in humans: Systematic review and implications for anxiety disorder research. *Behavior Therapy, 46,* 561–582. http://dx.doi.org/10.1016/j.beth.2014.10.001

Failing, M. F., & Theeuwes, J. (2015). Nonspatial attentional capture by previously rewarded scene semantics. *Visual Cognition, 23,* 82–104. http://dx.doi.org/10.1080/13506285.2014.990546

Gamberale-Stille, G., & Tullberg, B. S. (1999). Experienced chicks show biased avoidance of stronger signals: An experiment with natural colour

variation in live aposematic prey. *Evolutionary Ecology, 13,* 579–589. http://dx.doi.org/10.1023/A:1006741626575

Hickey, C., Kaiser, D., & Peelen, M. V. (2015). Reward guides attention to object categories in real-world scenes. *Journal of Experimental Psychology: General, 144,* 264–273. http://dx.doi.org/10.1037/a0038627

LaBar, K. S., Cook, C. A., Torpey, D. C., & Welsh-Bohmer, K. A. (2004). Impact of healthy aging on awareness and fear conditioning. *Behavioral Neuroscience, 118,* 905–915. http://dx.doi.org/10.1037/0735-7044.118.5.905

Le Pelley, M. E. (2010). Attention and human associative learning. In C. J. Mitchell & M. E. Le Pelley (Eds.), *Attention and associative learning: From brain to behavior* (pp. 187–215). New York, NY: Oxford University Press.

Le Pelley, M. E., Pearson, D., Griffiths, O., & Beesley, T. (2015). When goals conflict with values: Counterproductive attentional and oculomotor capture by reward-related stimuli. *Journal of Experimental Psychology: General, 144,* 158–171. http://dx.doi.org/10.1037/xge0000037

Li, W., Howard, J. D., Parrish, T. B., & Gottfried, J. A. (2008). Aversive learning enhances perceptual and cortical discrimination of indiscriminable odor cues. *Science, 319,* 1842–1845. http://dx.doi.org/10.1126/science.1152837

Lim, S. L., & Pessoa, L. (2008). Affective learning increases sensitivity to graded emotional faces. *Emotion, 8,* 96–103. http://dx.doi.org/10.1037/1528-3542.8.1.96

Lissek, S., Biggs, A. L., Rabin, S. J., Cornwell, B. R., Alvarez, R. P., Pine, D. S., & Grillon, C. (2008). Generalization of conditioned fear-potentiated startle in humans: Experimental validation and clinical relevance. *Behaviour Research and Therapy, 46,* 678–687. http://dx.doi.org/10.1016/j.brat.2008.02.005

Mathews, A., & MacLeod, C. (2005). Cognitive vulnerability to emotional disorders. *Annual Review of Clinical Psychology, 1,* 167–195. http://dx.doi.org/10.1146/annurev.clinpsy.1.102803.143916

McTeague, L. M., Gruss, L. F., & Keil, A. (2015). Aversive learning shapes neuronal orientation tuning in human visual cortex. *Nature Communications, 6,* 7823–7828. http://dx.doi.org/10.1038/ncomms8823

Notebaert, L., Crombez, G., Van Damme, S., De Houwer, J., & Theeuwes, J. (2011). Signals of threat do not capture, but prioritize, attention: A conditioning approach. *Emotion, 11,* 81–89. http://dx.doi.org/10.1037/a0021286

Öhman, A. (2009). Of snakes and faces: An evolutionary perspective on the psychology of fear. *Scandinavian Journal of Psychology, 50,* 543–552. http://dx.doi.org/10.1111/j.1467-9450.2009.00784.x

Onat, S., & Büchel, C. (2015). The neuronal basis of fear generalization in humans. *Nature Neuroscience, 18,* 1811–1818. http://dx.doi.org/10.1038/nn.4166

Resnik, J., Sobel, N., & Paz, R. (2011). Auditory aversive learning increases discrimination thresholds. *Nature Neuroscience, 14,* 791–796. http://dx.doi.org/10.1038/nn.2802

Rush, A. J., Trivedi, M. H., Ibrahim, H. M., Carmody, T. J., Arnow, B., Klein, D. N., . . . Keller, M. B. (2003). The 16-Item quick inventory of depressive symptomatology (QIDS), clinician rating (QIDS-C), and self-report (QIDS-SR): A psychometric evaluation in patients with chronic major depression. *Biological Psychiatry, 54,* 573–583. http://dx.doi.org/10.1016/S0006-3223(02)01866-8

Schechtman, E., Laufer, O., & Paz, R. (2010). Negative valence widens generalization of learning. *The Journal of Neuroscience, 30,* 10460–10464. http://dx.doi.org/10.1523/JNEUROSCI.2377-10.2010

Schmidt, L. J., Belopolsky, A. V., & Theeuwes, J. (2015). Attentional capture by signals of threat. *Cognition and Emotion, 29,* 687–694. http://dx.doi.org/10.1080/02699931.2014.924484

Smith, S. D., Most, S. B., Newsome, L. A., & Zald, D. H. (2006). An emotion-induced attentional blink elicited by aversively conditioned stimuli. *Emotion, 6,* 523–527.

Spielberger, C. D., Gorsuch, R. L., Lushene, R., Vagg, P. R., & Jacobs, G. A. (1983). *Manual for the state-trait anxiety scale.* Palo Alto, CA: Consulting Psychologists.

Theeuwes, J. (1991). Cross-dimensional perceptual selectivity. *Perception & Psychophysics, 50,* 184–193. http://dx.doi.org/10.3758/BF03212219

Theeuwes, J. (2010). Top-down and bottom-up control of visual selection. *Acta Psychologica, 135,* 77–99. http://dx.doi.org/10.1016/j.actpsy.2010.02.006

Van Bockstaele, B., Verschuere, B., Tibboel, H., De Houwer, J., Crombez, G., & Koster, E. H. (2014). A review of current evidence for the causal impact of attentional bias on fear and anxiety. *Psychological Bulletin, 140,* 682–721. http://dx.doi.org/10.1037/a0034834

van Meurs, B., Wiggert, N., Wicker, I., & Lissek, S. (2014). Maladaptive behavioral consequences of conditioned fear-generalization: A pronounced, yet sparsely studied, feature of anxiety pathology. *Behaviour Research and Therapy, 57,* 29–37. http://dx.doi.org/10.1016/j.brat.2014.03.009

Vuilleumier, P. (2005). How brains beware: Neural mechanisms of emotional attention. *Trends in Cognitive Sciences, 9,* 585–594. http://dx.doi.org/10.1016/j.tics.2005.10.011

Wyble, B., Folk, C., & Potter, M. C. (2013). Contingent attentional capture by conceptually relevant images. *Journal of Experimental Psychology: Human Perception and Performance, 39,* 861–871. http://dx.doi.org/10.1037/a0030517