

Conditioned Fear Modulates Visual Selection

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Eye movements reflect the dynamic interplay between top-down- and bottom-up-driven processes. For example, when we voluntarily move our eyes across the visual field, salient visual stimuli in the environment may capture our attention, our eyes, or modulate the trajectory of an eye movement. Previous research has shown that the behavioral relevance of a salient stimulus modulates these processes. This study investigated whether a stimulus signaling an aversive event modulates saccadic behavior. Using a differential fear-conditioning procedure, we presented a threatening (conditional stimulus: CS+) and a nonthreatening stimulus distractor (CS-) during an oculomotor selection task. The results show that short-latency saccades deviated more strongly toward the CS+ than toward the CS- distractor, whereas long-latency saccades deviated more strongly away from the CS+ than from the CS- distractor. Moreover, the CS+ distractor captured the eyes more often than the CS- distractor. Together, these results demonstrate that conditioned fear has a direct and immediate influence on visual selection. The findings are interpreted in terms of a neurobiological model of emotional visual processing.

Keywords: fear conditioning, saccade curvature, emotion, visual selection, eye movement

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Imagine walking in a crowded subway trying to find your way out. Your eyes search for the green exit signs while you attempt to ignore distracting information. Nevertheless, your eyes are sometimes captured by irrelevant information such as flickering neon lights or screaming billboards. Such oculomotor captures are due to the high visual salience of a stimulus in relation to its background (Itti & Koch, 2000), either in terms of color, luminance, motion, or orientation (Nothdurft, 2000). Attentional or oculomotor capture may occur irrespective of the task at hand (Theeuwes, 1992, 1994; but see Folk, Remington, & Johnston, 1992; Folk, Remington, & Wright, 1994), but top-down processes, such as task or behavioral relevance, enhance this so-called priority processing (Fecteau & Munoz, 2006). Likewise, emotional stimuli are also assumed to be prioritized by the visual system (for review, see Mather & Sutherland, 2011). In line with this idea, research has shown that threatening stimuli such as an angry face in a crowd (Hansen & Hansen, 1988; Öhman, Lundqvist, & Esteves, 2001; but see Becker, Anderson, Mortensen, Neufeld, & Neel, 2011), a snake in the grass (Öhman, Flykt, & Esteves, 2001; but see Lipp, Derakshan, Waters, & Logies, 2004; Tipples, Young, Quinlan,

Broks, & Ellis, 2002), or a man holding a knife (Blanchette, 2006) are detected faster than nonemotional stimuli (for review, see Yiend, 2010). However, the questions of how and when in time emotional stimuli modulate visual selection are still a matter of debate (de Gelder, van Honk, & Tamietto, 2011; Pessoa & Adolphs, 2010; Pourtois, Schettino, & Vuilleumier, in press).

One method to index the effect of emotion on attentional and visual selection is to investigate eye movement behavior. Despite the strong link between visual spatial attention and eye movements (Rizzolatti, Riggio, Dascola, & Umiltà, 1987), few studies on emotional attention have used eye movements. When available, they have mainly focused on saccade latency (e.g., Bannerman, Milders, de Gelder, & Sahraie, 2009; Bannerman et al., 2010a, 2010b; Belopolsky, Devue, & Theeuwes, 2011; Kissler & Keil, 2008) or viewing patterns, such as first fixations or fixation duration in free-viewing or visual search paradigms (e.g., Calvo & Lang, 2004; Humphrey, Underwood, & Lambert, 2012; Nummenmaa, Hyona, & Calvo, 2006). These studies have found faster saccades toward and more fixations on emotional compared with nonemotional pictures. However, the emotional information in these studies is never completely task-irrelevant, leaving open the question of whether emotional visual stimuli are automatically prioritized by the visual system (Hodsoll, Viding, & Lavie, 2011). For example, in the study of Calvo and Lang (2004), the emotional stimulus was also a target stimulus, and was therefore task-relevant. In the study by Bannerman et al. (2010b), the emotional stimulus was presented at the same location as the target stimulus and was therefore also task-relevant to some extent.

A well-validated eye movement paradigm to investigate the influence of task-irrelevant information on visual selection is the oculomotor selection task (Van der Stigchel, 2010; Van der Stigchel, Meeter, & Theeuwes, 2006). In this task, participants are instructed to make a simple saccade from a fixation cross to a

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target stimulus while a visual distractor is presented close to the target. Research has consistently revealed that salient distractors modulate the trajectory of the saccade to the target stimulus (Doyle & Walker, 2001; Godijn & Theeuwes, 2004; Ludwig & Gilchrist, 2003; Van der Stigchel et al., 2006). Such modulation is believed to occur because spatial attention is allocated to the distractor location (Sheliga, Riggio, & Rizzolatti, 1994; Van der Stigchel & Theeuwes, 2005). It is noteworthy that this modulation shows a linear relation with saccade latency: Saccades that are initiated shortly after stimulus onset tend to deviate toward a distractor, whereas saccades initiated later (after 200 ms) tend to deviate away from the distractor (McSorley, Haggard, & Walker, 2006). These phenomena have been explained by competing activity between the target and distractor locations in the oculomotor system. Presaccadic activity of neurons signaling the target location is averaged with activity of neurons signaling the distractor location. Therefore, a saccade will deviate toward the distractor when a saccade is generated early after stimuli onset (McPeck, 2006; McPeck, Han, & Keller, 2003). Subsequently, a top-down process suppresses the activity at the distractor location (McSorley et al., 2006). Due to this inhibition, the saccade vector deviates away from the distractor location; hence, saccades generated later after stimuli onset will deviate away from a distractor (Van der Stigchel et al., 2006; Walker & McSorley, 2008; Walker, McSorley, & Haggard, 2006). Erroneous saccades that land on the distractor stimulus (oculomotor capture) are explained by faster bottom-up driven activity at the distractor location relative to the slower top-down driven activity at the target location (Godijn & Theeuwes, 2002). Two studies (Nummenmaa, Hyona, & Calvo, 2009, Experiment 3; Schmidt, Belopolsky, & Theeuwes, 2012) have used the oculomotor selection task with an emotional distractor. Both reported that the trajectory of the saccades deviated more strongly away from an emotional distractor than from a neutral distractor. As the mean saccade latencies in the Nummenmaa et al. (2009) and Schmidt et al. (2012) studies were longer than 200 ms, the to-be-expected result is indeed a deviation away from the distractor.

The main objective of our study was to investigate the time course of emotional modulation on saccade trajectories. More specifically, we were interested whether saccades that are initiated shortly after stimulus onset (short-latency saccades) would result in stronger deviation toward the emotional-laden distractor than the neutral distractor, or would even result in oculomotor capture, and whether long-latency saccades would result in stronger deviation away from the emotional-laden distractor. To generate short-latency and long-latency saccades, we varied the gap between the offset of the fixation cross and the onset of the target stimulus (McSorley et al., 2006; Munoz, Dorris, Pare, & Everling, 2000; Saslow, 1967). Previous research has revealed that saccade latencies decrease when the time between fixation offset and target onset becomes longer, and saccade latencies increase when the fixation cross and target presentation overlap in time. To create a threatening distractor, we used a differential fear-conditioning procedure (Mackintosh, 1983). This procedure has proven successful in emotional attention research. For example, behavioral studies have shown that fear-conditioned stimuli are detected faster than neutral stimuli (Öhman & Mineka, 2001) and are associated with enhanced activation of a frontoparietal network that is also involved in spatial attention (Armony & Dolan, 2002). Moreover,

fear-conditioned stimuli are associated with enhanced processing in visual cortex (Lim, Padmala, & Pessoa, 2009; Stolarova, Keil, & Moratti, 2006) and with enhanced amygdala activation (Davis & Whalen, 2001; Lim et al., 2009). The amygdala is an important subcortical brain structure in emotion processing and is believed to bias perception in favor of emotional stimuli via direct connections to the visual cortex (Vuilleumier, 2005; Vuilleumier, Armony, & Dolan, 2004). For example, Stolarova et al. (2006) showed that the earliest visual component (C1), which is thought to originate from striate cortex, is modulated by fear-conditioned stimuli (see also Pourtois, Grandjean, Sander, & Vuilleumier, 2004). Moreover, in binocular rivalry fear-conditioned stimuli predominate neutral stimuli, a process that is believed to occur through direct connections from the amygdala to the visual cortex (Alpers, Ruhleder, Walz, Muhlberger, & Pauli, 2005). It is of interest that the latter two studies (Alpers et al., 2005; Stolarova et al., 2006) used conditioned stimuli that were initially neutral (e.g., gratings), suggesting that there is no need to use biologically relevant stimuli as conditioned stimuli to observe effects of fear on attention procedure. In our conditioning procedure, we used initially neutral stimuli: One of two colored circles (conditioned stimulus: CS+) was associated with an aversive noise (unconditioned stimulus: US), whereas the other colored circle (CS-) was not.

The use of a fear-conditioning paradigm has two advantages in comparison with previous research. First, emotional distractors are signals of a genuine threat instead of symbolic representations of threat (e.g., pictures). Second, the stimulus features of the distractor are under experimenter control, allowing for a comparison that is not influenced by potential visual differences between stimuli (e.g., Calvo & Nummenmaa, 2008; Hunt, Cooper, Hungry, & Kingstone, 2007). As saccade deviation reflects the amount of competition within the oculomotor system (Godijn & Theeuwes, 2004), we expected that the threatening distractor (CS+) would be a stronger competitor for visual selection than the nonthreatening distractor (CS-); hence, we expected that saccades generated early in time (short-latency saccades) would deviate more strongly toward the threatening distractor than the nonthreatening distractor and saccades generated later in time (long-latency saccades) would deviate more strongly away from the threatening distractor than the nonthreatening distractor. In addition, we expected the threatening distractor to capture the eyes more often than the nonthreatening distractor.

Experiment 1

Method

Participants, apparatus, and design. Eleven participants were seated 65 cm from a computer screen with their head positioned on a chin rest. Eye movements were registered by means of a video-based eye tracker (SR Research Ltd., Kanata, Ontario, Canada), which has a 1000-Hz temporal and a 0.025° spatial resolution. Participants fixated a center fixation cross on a black background (see Figure 1a). After 1,000 ms, the target, a light gray-filled circle with a diameter of 1.44°, appeared either 9.3° above or below the fixation point. The fixation cross was removed at different stimulus onset asynchronies (SOAs) of -150, -50, 0, 50, and 150 ms relative to target onset to manipulate saccade latency. In 80% of the trials, a distractor, either a red- or a

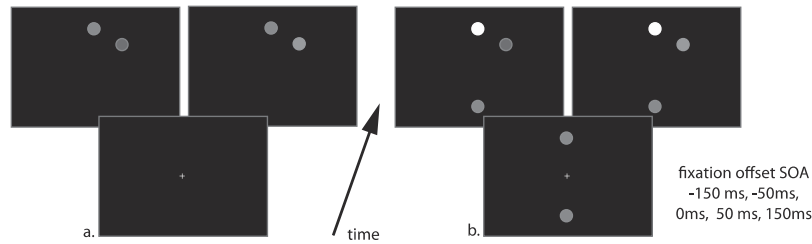


Figure 1. From bottom to top, succession of events in a trial in which the target is presented above fixation point (on the vertical meridian) while a colored circle distractor (either a CS+ or CS-) is presented. (a) Experiment 1. (b) Experiment 2. For a color version of this figure, please see the supplemental materials link on the first page of this article.

green-filled circle (1.44° in diameter) was presented simultaneously at 8.2° from the target. The vertical distance of the distractor from fixation was 5.39° , whereas it was 3.91° from the target. The horizontal distance of the distractor from fixation and from the target was 7.18° . After 2,000 ms, the stimuli were removed from the screen and the next trial started. *Figure 1a* shows the sequence of a trial with a distractor and fixation offset at target onset.

Procedure. Before the experiment, a differential fear-conditioning procedure was started in which the distractors were presented one by one. One of the colors (CS+) was paired with an aversive noise (US), whereas the other color (CS-) was not. Five participants were presented with a red CS+ and a green CS- and six participants vice versa. The US consisted of a 200-ms 100-dB white noise for half of the participants and (due to technical problems) a 50-ms 100-dB white noise for the other half.¹ The US was presented 250 ms after CS+ onset. When participants were able to correctly identify the color that predicted the noise, the experiment started.

In the experiment, participants were required to make a speeded saccade to the target while ignoring the presence of a distractor. Each participant performed 200 experimental trials. Furthermore, eight additional reinforcement trials in which the CS+ was presented together with the US were randomly mixed with the experimental trials to avoid extinction (Mackintosh, 1974). The timing of the US was the same as in the fear-conditioning procedure, which was 250 ms after CS+ onset. The reinforcement trials were not further analyzed. Afterward, ratings of fear of the CS+ and CS- and ratings of the intensity, unpleasantness, and expectancy of the US were obtained using Likert scales (1 = *not at all* to 9 = *extremely*).

Data analyses. The initial saccade starting position had to be within 1° horizontal and 2° vertical from the center fixation point. The initial saccade was assigned to a target if the endpoint of the initial saccade was within 4° of the center of the target position and to a distractor if the endpoint was within 4° of the center of the distractor position. Too small saccades ($<3^\circ$) were considered errors and were excluded from analyses. Saccade latencies shorter than 80 ms or longer than 600 ms were also considered errors and were excluded from analyses. Latencies shorter or longer than 2.5 standard deviations from the mean latency were considered outliers and were excluded from analyses.

Saccade trajectories were examined by calculating the mean angle of the actual saccade path relative to the mean angle of a straight line between the starting point of the saccade and the saccadic target. The angle of the actual saccade was calculated for

each 2-ms sample point by examining the angle of the straight line between fixation and the current sample point. Angles were averaged across the whole saccade and subtracted from the angle of the straight line between fixation and the target location. To compute the influence of the distractor on saccade trajectories, we compared each saccade in a trial with a distractor with that of the averaged mean path angles of all trials without a distractor to determine whether the saccade in the presence of a distractor deviated toward or away from the location of the distractor. Deviations were signed so that a positive value indicated deviation toward the distractor and a negative value indicated deviation away. All deviations are given in radians (for a review of the various measures used in the literature, see Van der Stigchel et al., 2006).

To examine the time course of oculomotor competition, we calculated individual cumulative distribution functions of the saccade latency for each participant and each condition (CS+ or CS-). These were averaged in four bins using the vincerizing procedure (Ratcliff, 1979). Therefore, the first bin contained the fastest saccades, and the last bin contained the slowest saccades. For each participant and condition, each bin contained a minimum of 12 trials and a maximum of 20 trials, depending on the number of correct trials for each participant and condition. When the number of trials was not even, the last bins could contain one trial more than the others.

Results

Excluded trials. Two participants were removed from analyses because of bad calibration or too many excluded trials based on the described definitions in the data analyses ($>35\%$ excluded trials). Of the remaining nine participants, 19.3% of all trials were removed. There was no significant difference between percentages of excluded trials in the threatening condition (18.5%) compared with the nonthreatening condition (20%; $p = .44$).

Fear conditioning. Mean ratings of intensity, unpleasantness, and fear of the US were 7.7, 7.1, and 5.8, respectively. Participants rated fear of the CS+ ($M = 5.1$) higher than that of the CS- ($M = 1.6$; two-related Wilcoxon's test, $p < .01$). Furthermore, expectancy rating of the US after a CS+ ($M =$

¹ A repeated measures ANOVA on saccade deviation with US (200 ms or 50 ms) as the between-subjects factor and bin (1, 2, 3 or 4) and signal (CS+, CS-) as the within-subjects factors revealed no interaction with saccade deviation ($p = .16$) or saccade latency ($p = .7$). Therefore, data from both groups were collapsed.

4.8) was higher than after a CS− ($M = 1.9$; two-related Wilcoxon's test, $p < .01$). These results suggest that our fear-conditioning procedure was successful.

Eye movement behavior. Figure 2 shows the mean saccade latency and deviation per condition per bin. An analysis of variance (ANOVA) on saccade latency with bin (1, 2, 3, and 4) and signal (CS+ or CS−) as factors revealed a main effect of bin, $F(3, 24) = 85.2$, $p < .01$ (with Greenhouse–Geisser correction), but no main effect of signal ($F < 1$) and no interaction between signal and bin ($p > .3$).

A similar ANOVA on saccade deviation revealed no main effect of bin ($p = .1$), no interaction between signal and bin ($p > .2$), but a significant main effect of signal, $F(1, 8) = 9.02$, $p < .05$. As can be seen in Figure 2, the saccades deviated more strongly toward the CS+ distractor than toward the CS− distractor.

Furthermore, significantly more saccades landed on the CS+ distractor (9.3%) than on the CS− distractor (3.3%; two-related Wilcoxon's test, $p < .05$).

Discussion

Our results clearly indicate a modulation of visual selection induced by a threatening distractor. The saccade deviation toward the threatening distractor (CS+) was stronger relative to the non-threatening distractor (CS−). Moreover, the threatening distractor captured the eyes more often than the nonthreatening distractor. Together, these results suggest that threatening information has a direct low-level impact on the oculomotor system modulating visual selection early in time.

In contrast to previous studies that found deviation away from a threatening distractor (Nummenmaa et al., 2009; Schmidt et al., 2012), we found deviations toward the distractor stimuli. As discussed in the introduction, previous research has shown a linear relation between trajectory deviation and saccade latency; a deviation toward a distractor is followed by a deviation away after approximately 200 ms (McSorley, 2006). Indeed, the mean latencies in the Nummenmaa et al. (2009) and Schmidt et al. (2012) studies were longer than 200 ms. Our results show that the slowest saccades (Bin 4) curved less toward the distractor than the fastest saccades (Bin 1), although the interaction was not significant.

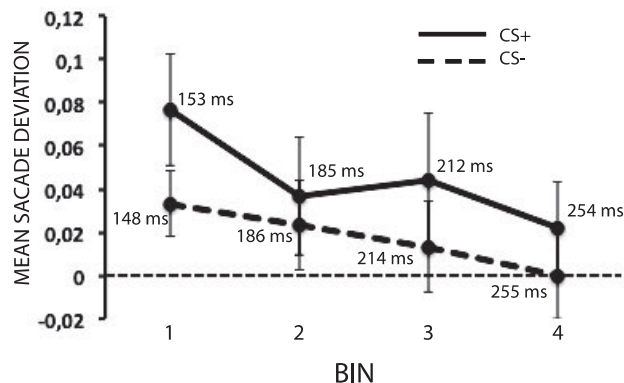


Figure 2. Mean saccade deviation and mean saccade latency for the CS+ and CS− distractor per bin. Error bars represent normalized standard errors.

Moreover, the mean saccade latencies in all bins in Experiment 1 were relatively short. This was probably due to the highly salient signal at the top or the bottom of the visual field of the two sudden onsets signaling target and distractor location. Sudden onsets (luminance increments) are known to be highly salient (Yantis & Jonides, 1984). Therefore, in Experiment 2, we wanted to increase saccade latency by decreasing the visual salience at the target location. We therefore expected to find slower saccade latencies and hence deviations away from the distractor in the last bin. Similar to Experiment 1, we expected the threatening distractor to be a stronger competitor for visual selection than the nonthreatening distractor, therefore evoking stronger deviations and capturing the eyes more often than the nonthreatening distractor. Furthermore, we wanted to replicate the results from Experiment 1 with a US that was the same for all participants.

Experiment 2

Method

Participants, apparatus, and design. Twenty participants were seated 65 cm from a computer screen with their head positioned on a chin rest. Participants fixated a center fixation cross on a black background. At a distance of 9.3° above and below the fixation point, a placeholder, a light gray-filled circle with a diameter of 1.44° , was presented (see Figure 1b). After 1,000 ms, one of the placeholders changed to white, indicating the target location. The fixation cross was removed at different SOAs of -150 , -50 , 0 , 50 , and 150 ms relative to target onset. In 80% of the trials, a distractor, either a red- or a green-filled circle (1.44° in diameter), was presented simultaneously at 8.2° from the target. The vertical distance of the distractor from fixation was 5.39° , whereas it was 3.91° from the target. The horizontal distance of the distractor from fixation and from the target was 7.18° . After 2,000 ms, the stimuli were removed from the screen and the next trial started. Figure 1b shows the sequence of a trial with a distractor and fixation offset at target onset.

Procedure and data analyses. The same procedure and data analyses as in Experiment 1 were used, except that the US consisted of a 200-ms 100-dB white noise for all participants.

Results

Excluded trials. Three participants were removed from analyses because of bad calibration or too many excluded trials based on the described definitions (>35% excluded trials). Of the remaining 17 participants, 22.9% of all trials were removed. A two-related Wilcoxon's test showed that more trials were excluded in the threatening condition (24.8%) compared with the nonthreatening condition (21%; $p < .05$).

Fear conditioning. Mean ratings of intensity, unpleasantness, and fear of the US were 6.8, 6.9, and 6.1, respectively. Participants rated fear of the CS+ ($M = 4.9$) higher than that of the CS− ($M = 1.2$; two-related Wilcoxon's test, $p < .01$). Furthermore, expectancy rating of the US after a CS+ ($M = 4.9$) was higher than after a CS− ($M = 1.3$; two-related Wilcoxon's test, $p < .01$). These results indicate that our fear-conditioning procedure was successful.

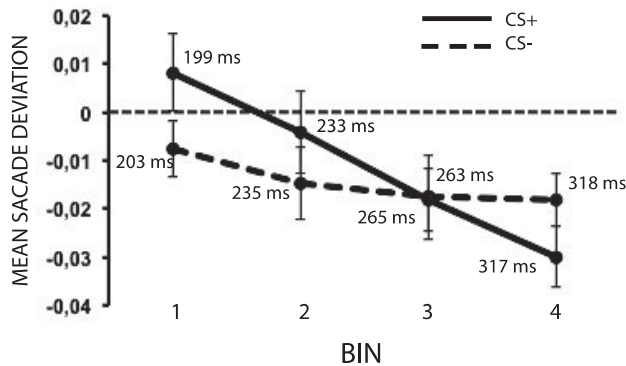


Figure 3. Mean saccade deviation and mean saccade latency for the CS+ and CS- distractor per bin. Error bars represent normalized standard errors.

Eye movement behavior. Figure 3 shows the mean saccade latency and deviation per condition per bin. An ANOVA on saccade latency with bin (1, 2, 3, and 4) and signal (CS+ and CS-) as factors revealed a main effect of bin, $F(3, 48) = 288.86$, $p < .01$ (with Greenhouse-Geisser correction), but no main effect of signal ($p > .29$) and no interaction between signal and bin ($F < 1$).

A similar ANOVA on saccade deviation revealed a main effect of bin, $F(3, 48) = 7.29$, $p < .01$ (with Greenhouse-Geisser correction), no main effect of signal ($F < 1$), but a significant interaction between signal and bin, $F(3, 48) = 2.9$, $p < .05$ (with Greenhouse-Geisser correction). A trend analysis with signal (CS+ and CS-) and bin (1, 2, 3, and 4) as factors revealed no main effect of signal ($F < 1$), a significant main effect of bin, $F(1, 16) = 25.3$, $p < .01$, and a significant interaction between signal and bin, $F(1, 16) = 7.52$, $p < .05$. As can be seen in Figure 3, the linear trend is steeper for the threatening distractor condition, $F(1, 16) = 19.9$, $p < .01$, than for the nonthreatening distractor condition, $F(1, 16) = 3.7$, $p = .07$, indicating that the threatening distractor had a stronger effect over time on saccade deviation than the nonthreatening distractor.

Subsequent planned comparisons showed a marginally significant difference in the first bin, $t(16) = 1.7$, $p = .06$, one-tailed, due to stronger deviation toward a threatening distractor relative to a nonthreatening distractor and a significant difference in the last bin, $t(16) = 2.1$, $p < .05$, one-tailed, due to stronger deviations away from the threatening distractor relative to a nonthreatening distractor.

The two-related Wilcoxon's test on percentage of oculomotor capture between the nonthreatening (3.4%) and the threatening distractor (4.1%) did not reach significance.

Discussion

The results of Experiment 2 show a modulation of visual selection induced by a threatening distractor: Short-latency saccades deviated more strongly toward the threatening distractor (CS+), whereas long-latency saccades deviated away more strongly from the threatening distractor relative to the nonthreatening distractor (CS-). The stronger deviations toward the threatening distractor (CS+) for the short-latency saccades are consistent with the results

of Experiment 1, indicating that the effects do not seem to be dependent on particular US characteristics. Furthermore, the lack of an effect of threat on saccade latency is also consistent with Experiment 1. However, as predicted, saccade latencies in Experiment 2 were increased relative to Experiment 1. Probably this was due to the less salient stimulus signaling the target location; a color change instead of a sudden onset. Consistent with previous studies on saccadic behavior with a mean latency of more than 200 ms (Nummenmaa et al., 2009; Schmidt et al., 2012), we found emotional modulation of the saccade deviation away from the distractor for the slowest saccades.

General Discussion

The present study investigated the time course of emotional modulation on saccade trajectories. Either a threatening or a non-threatening distractor was presented close to a neutral target to induce oculomotor competition. It was predicted that the threatening distractor (CS+) would be a stronger competitor for visual selection than the nonthreatening distractor (CS-) and therefore would result in stronger deviations. Consistent with our prediction, results from Experiments 1 and 2 together show that threatening information modulates short-latency as well as long-latency saccades. Short-latency saccades deviated more strongly toward a threatening distractor, whereas long-latency saccades deviated more strongly away from a threatening distractor relative to a nonthreatening distractor. In addition, in Experiment 1, the threatening distractor captured the eyes more often than the nonthreatening distractor. This pattern of results is consistent with earlier studies that manipulated the salience of the distractor by making it more or less relevant (Hickey & van Zoest, 2012; Mulckhuyse, Van der Stigchel, & Theeuwes, 2009). The reason why we did not find a significant difference in oculomotor capture in Experiment 2 was probably due to the increased latencies of the saccades. Previous research has showed that oculomotor capture occurs more often when saccades are initiated shortly after the distractor is presented (Godijn & Theeuwes, 2002; Mulckhuyse, Van Zoest, & Theeuwes, 2008).

In both experiments, saccade latency was not affected by threatening information, suggesting that the stronger deviations in the threatening condition cannot be explained by differences in saccade latency. The absence of an effect on saccade latency is not consistent with a previous study investigating emotional modulation of saccade trajectory and latency (West, Al-Aidroos, Susskind, & Pratt, 2011). In contrast, West et al. (2011) found emotional modulation of saccade latency but not on saccade trajectory. Consequently, they concluded that temporal rather than spatial programming in the oculomotor system is affected by threatening information. However, in their study, the threatening stimulus, an angry face, was presented at fixation, and both the target and the distractor consisted of neutral stimuli. Therefore, the different stimulus configuration is probably the cause for the discrepant findings. Future research with threatening stimuli in different stimulus configurations may further elucidate the temporal and spatial aspects of saccade programming in the presence of threat.

The results from Experiment 1 revealed that a task-irrelevant threatening distractor has an immediate and direct influence on visual selection. This indicates that very early in time the oculomotor system differentiates between a threatening and a nonthreat-

ening stimulus. In contrast to the more complex emotional stimuli used in the studies by Nummenmaa et al. (2006) and Schmidt et al. (2012), our stimuli did not request high-level processing. Visual information is processed from lower to higher cortical areas during the so-called feed-forward sweep (Lamme & Roelfsema, 2000). Moreover, visual information is processed via several pathways, including a subcortical pathway. The subcortical pathway is supposed to subserve automatic detection of threat (LeDoux, 2000; Liddell et al., 2005; Morris, Öhman, & Dolan, 1999) and is thought to be involved in affective blindsight (de Gelder, Vroomen, Pourtois, & Weiskrantz, 1999; Jolij & Lamme, 2005). From an evolutionary viewpoint, it is believed that this pathway processes biological relevant stimuli, such as angry faces or spiders (Öhman et al., 2001a), but it has also been implicated in fear conditioning (Hamm et al., 2003; LeDoux, 2000). For instance, in a study by Hamm et al. (2003), a patient with bilateral cortical damage to the visual cortex was able to acquire a fear response to a fear-conditioned visual stimulus that he could not consciously perceive. The subcortical pathway includes structures such as the superior colliculus and the pulvinar, essential for oculomotor behavior (for review, see Schall, 1995), and the amygdala, which is known to be vital in the acquisition and expression of conditioned fear (Davidson & Irwin, 1999; Davis, 1992a, 1992b). Activity at the distractor location in the oculomotor system, which caused the eyes to deviate more strongly toward the threatening stimulus, may thus be enhanced directly because of the reciprocal connection between the superior colliculus, pulvinar, and amygdala (Linke, De Lima, Schwegler, & Pape, 1999; see also West et al., 2011). However, the superior colliculus is not the only subcortical structure that is essential in oculomotor behavior. For instance, the pulvinar has been associated with saccadic behavior (Robinson & McClurkin, 1989) and, in addition, with the prioritization processing of emotional visual stimuli (Pessoa & Adolphs, 2010). Furthermore, higher visual areas, such as the frontal eye fields (FEFs), also play an essential role in oculomotor programming (Schall, 1995) and in saccade deviations away from a distractor (McSorley et al., 2006). Moreover, the FEFs are believed to be involved in the activation of possible target locations (McPeck, 2006; Walker, Techawachirakul, & Haggard, 2009) and are part of the so-called saliency map (Munoz, 2002; Thompson & Bichot, 2005) or priority map (Fecteau & Munoz, 2006). Fecteau and Munoz (2006) argued that top-down information, such as behavioral relevant information, integrates with bottom-up saliency information onto a priority map. The underlying mechanisms of the priority map may be the oculomotor network, including areas such as the superior colliculus, the pulvinar, and the FEF. The current study shows that conditioned fear has a direct and immediate influence on visual selection processes, reflected by stronger deviations toward and away from a threatening distractor. However, how emotional stimuli modulate these visual selection processes is still unclear. More research is needed to elucidate the underlying neural mechanisms in visual processing of emotional stimuli.

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