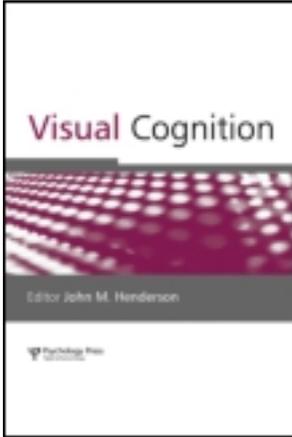


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Lisette J. Schmidt^a, Artem V. Belopolsky^a & Jan Theeuwes^a

^a Department of Cognitive Psychology, Vrije Universiteit Amsterdam, The Netherlands

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The presence of threat affects saccade trajectories

Lisette J. Schmidt, Artem V. Belopolsky, and Jan Theeuwes

Department of Cognitive Psychology, Vrije Universiteit Amsterdam,
The Netherlands

In everyday life, fast identification and processing of threat-related stimuli is of critical importance for survival. Previous studies suggested that spatial attention is automatically allocated to threatening stimuli, such as angry faces. However, in the previous studies the threatening stimuli were not completely irrelevant for the task. In the present study we used saccadic curvature to investigate whether attention is automatically allocated to threatening emotional information. Participants had to make an endogenous saccade up or down while an irrelevant face paired with an object was present in the periphery. The eyes curved away more from the angry faces than from either neutral or happy faces. This effect was not observed when the faces were inverted, excluding the possible role of low-level differences. Since the angry faces were completely irrelevant to the task, the results suggest that attention is automatically allocated to the threatening stimuli, which generates activity in the oculomotor system, and biases behaviour.

Keywords: Attention; Emotion; Eye movements.

It is well-known that salient events in our environment may grab our attention or even our eyes even in situations where we try to look for something else (Theeuwes, Kramer, Hahn, & Irwin, 1998). Unexpected, novel, and salient events receive high priority in the brain. An important question is whether potentially dangerous events are also prioritized in visual selection. For example, our brain may be wired in such a way that a threatening facial expression receives processing priority. From an evolutionary perspective, fear may have evolved from preparatory states evoked by threat cues, in which survival depends on execution or inhibition of overt behaviour (Lang,

Please address all correspondence to Lisette Schmidt, Department of Cognitive Psychology, Vrije Universiteit Amsterdam, Van der Boeorchorststraat 1, 1081 BT Amsterdam, The Netherlands. E-mail: l.j.schmidt@vu.nl

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Davis, & Öhman, 2000). Fast identification of threat-related stimuli may therefore give an evolutionary advantage and improve chances of survival (LeDoux, 1996).

At a neural level it has been suggested that the amygdala, a subcortical structure specialized in detection of potentially dangerous events, might be involved in the prioritized processing of threat-related information. It is assumed that the amygdala participates in recognition of emotional signals via two pathways: A slower cortical route via the visual cortex, and a faster subcortical route via the superior colliculus (SC) and the pulvinar (LeDoux, 1996).

Evidence from both behavioural and neuroimaging studies suggests that threat-related stimuli receive priority in visual selection. For example, visual search experiments revealed that detection of a fear-relevant stimulus embedded in a background of neutral distractors is usually more quick than detecting a neutral stimulus in a background of neutral stimuli (e.g., Öhman, Flykt, & Esteves, 2001; Rinck, Becker, Kellerman, & Roth, 2003; Soares, Estevez, Lundqvist, & Öhman, 2009). A similar pattern of results with displays of faces with emotional expressions is found in a study by Fox et al. (2000), where participants were faster in responding to a single angry expression in a background of neutral faces compared to a single happy expression in a background of neutral faces.

An attentional bias for threatening stimuli is also revealed by spatial cueing tasks (see Posner, 1980). When a threatening cue that could be presented at one of the two locations was followed by a target at the same location (i.e., valid trials), this resulted in faster responses relative to a neutral cue. Moreover, when a threatening cue was at a different location than the target (i.e., invalid trials), slower responses relative to neutral cue trials were observed (e.g., Fox, Russo, Bowles, & Dutton, 2001).

The findings from visual search and cueing paradigms have generally been interpreted as evidence that fear-related stimuli capture attention in an automatic bottom-up fashion (e.g., Mathews, Mackintosh, & Fulcher, 1997; Öhman, Flykt, & Esteves, 2001; Öhman, Lundqvist, & Esteves, 2001). However, the interpretation of these results is limited given that, in both visual search and cueing paradigms, threatening stimuli remain somewhat relevant for the task goal. Specifically, in the visual search task the threatening stimulus is also a target of search, and in the cueing tasks the target usually appears at the location of the threatening stimulus with 50% probability, not discouraging participants to adopt a strategy of actively attending to it. Therefore, the view that threat-related stimuli automatically receive priority in visual selection remains unresolved.

One way to examine this issue is to investigate how the mere presence of threatening stimuli affects overt behaviour, such as for example eye movements. It has been established that covert spatial attention is closely related

to saccadic eye movements. The premotor theory of attention (Rizzolatti, Riggio, Dascola, & Umiltà, 1987) states that the mechanisms responsible for covert attention and the mechanisms involved in programming saccadic eye movements are basically the same (Belopolsky & Theeuwes, 2009). In support of this view it has been demonstrated that saccade trajectories are affected by allocation of spatial attention (Sheliga, Riggio, & Rizzolatti, 1994; Van der Stigchel & Theeuwes, 2005). Specifically, it has been demonstrated that saccades tend to curve away from locations of salient but irrelevant distractors (Doyle & Walker, 2001; Godijn & Theeuwes, 2002, 2004; Ludwig & Gilchrist, 2003). For example, Godijn and Theeuwes (2004) demonstrated that saccades curved away more from onset distractors than from colour distractors, suggesting that increased saliency of a distractor leads to stronger saccade deviations. Moreover, Ludwig and Gilchrist (2003) demonstrated that although delayed saccadic responses can be influenced by top-down input, the initial saccadic response to the onset of a distractor is stimulus driven. Therefore, saccade curvature provides an ideal measure for examining automatic allocation of attention to irrelevant threatening stimuli. If a threatening face causes activity in the oculomotor system at the same moment that a saccade to another location has to be made, one expects that this activity needs to be suppressed, causing the eyes to curve away from the location of the threatening face.

In the present study participants had to make an endogenous saccade up or down while an irrelevant face paired with an object was present in the periphery. The face could have either an angry, happy, or neutral expression, while its location and content were completely irrelevant to the task. In order to control for low-level differences among facial expressions we have included a condition in which all stimuli were inverted. If threatening events indeed receive priority in visual selection over neutral events, then a threat-related distractor would lead to larger curvature away than an emotionally neutral distractor or any other emotional face or an inverted face.

EXPERIMENT 1

Method

Twenty naïve students from the VU University Amsterdam (16 females, mean age 22.4) participated in return for course credits or cash. All participants reported having normal or corrected-to-normal vision. Participants were seated 75 cm from a computer screen with their head positioned on a chinrest. Eye movements of the right eye were recorded with an EyeLink 1000 tracker (SR Research Ltd, Canada), with 1000 Hz temporal and 0.2° spatial resolution. An automatic algorithm detected saccades using minimum velocity and acceleration criteria of $35^\circ/\text{s}$ and $9500^\circ/\text{s}^2$, respectively.

Distractor stimuli consisted of emotional male faces and neutral objects. Faces were three male models from the Radboud Faces Database (RaFD; Langner et al., 2010). The neck and clothing were removed and the pictures were resized to $2.6^\circ \times 3.8^\circ$. Each model showed three affective expressions (angry, neutral, and happy), resulting in a total of nine face stimuli. Nine pictures of neutral objects (three houses, three fruits, and three kitchen supplies) were used to create pairs with the face stimuli. All stimuli were greyscale, equalized in contrast and brightness, and displayed against a white background. Pairing faces with objects was necessary because it has previously been shown that the presence of a single irrelevant distractor consistently leads to curvature away from the distractor location (Doyle & Walker, 2001). We therefore believe that presenting a single face as a distractor would lead to curvature away from that location, regardless of the facial expression. Therefore, pairing with an object of same size and luminance was necessary to avoid ceiling effects and to reveal differences between curvatures away from emotional expressions.

The experiment started with a nine-point grid calibration procedure, followed by a practice session of 24 trials and an experimental session of 432 trials. A trial started with the presentation of a central fixation cross ($0.5^\circ \times 0.5^\circ$) and two additional markers straight below and above the fixation. These markers were visible throughout the whole trial. After a random time between 800 and 1300 ms, an arrow (1.5°) was presented at the fixation, pointing either straight up or straight down with an equal probability. Simultaneously with the arrow, two distractor stimuli (one face and one object) appeared on the left and right sides of the screen, at 7° from fixation, measured from the centre of the pictures (see Figure 1). The face could appear on either the left or right side of the screen with an equal probability. The stimuli always appeared in the same hemifield where the eye movement had to be made.

Participants were instructed to immediately make a saccade in the direction of the arrow to the marker placed at the top or bottom of the display. Participants were informed that all distractors were irrelevant to the task. The order of stimulus presentation was randomized and there was an equal number of different emotional expressions and objects in a block of trials. Ten participants were presented with pictures with an upright orientation, and 10 other participants were presented with the same pictures, but inverted. The between-subject manipulation was chosen in order to avoid potential carryover effects that upright faces could have on the processing of inverted faces.

Data analysis. Saccade latency was defined as the interval between arrow onset and initiation of a saccadic eye movement. Trials in which saccade latency was lower than 80 ms or higher than 600 ms were removed

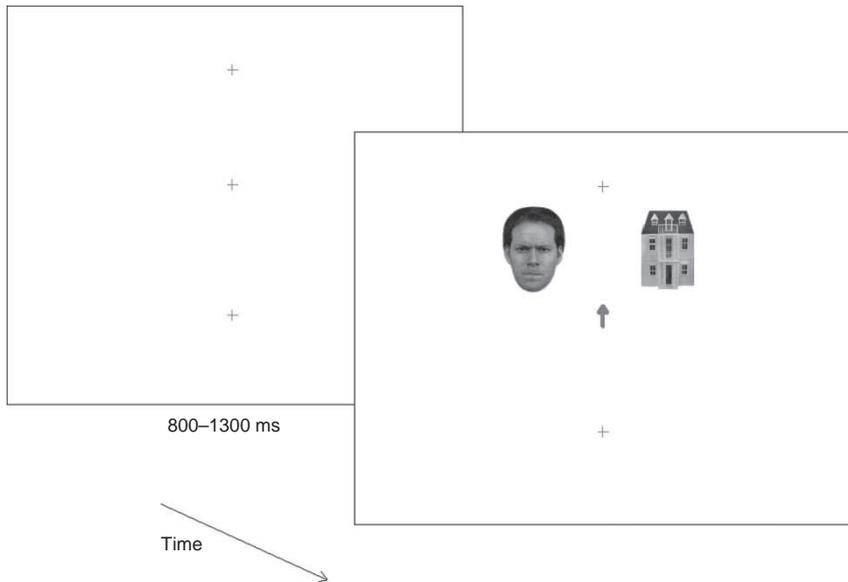


Figure 1. Schematic representation of a trial in Experiment 1. The task started with the presentation of a fixation cross ($0.5^\circ \times 0.5^\circ$), and two crosses 9° below and above fixation. Next, an arrow (1.5°) appeared at fixation, and participants had to make a speeded saccade to the indicated cross. Simultaneously with presentation of an arrow, a face and an object appeared in the periphery, at 7° from fixation.

from the analysis. Trials in which no saccades or small saccades ($<3^\circ$) were made were excluded from further analysis. If the endpoint of the saccade deviated less than 30° of arc from the centre of the target, the saccade was classified as correct and further analysed. To determine the influence of emotional expressions on saccade trajectory, we calculated the angular deviation of the saccade path for each 1 ms sample point that was greater than 0.5° from the central fixation and smaller than 0.5° from the endpoint of the saccade, relative to a straight line from the starting point of the saccade to the saccade endpoint. A median of these deviations was calculated for each saccade, averaged across saccade direction and normalized to the top hemifield (curvature for face presented on the left minus curvature for face presented on the right; for a similar method see Belopolsky & Theeuwes, 2011, and Van der Stigchel, Meeter, & Theeuwes, 2006). As a result, positive deviation difference values would indicate an overall curvature away from the face location; negative values would indicate an overall curvature towards the face location. Saccade curvatures were analysed for each emotional expression (angry, neutral, and happy) separately.

Results and discussion

Based on the criteria described earlier, 4.7% of the trials in the upright condition and 5.8% of the trials in the inverted condition were excluded from analyses. The number of excluded trials did not differ as a function of distractor face.

The mean saccade curvatures for the upright and inverted stimuli conditions are presented in Figure 2. A mixed-effects ANOVA with condition (upright or inverted) as between-subjects factor and emotional expression (angry, happy, or neutral) as within-subjects factor showed a significant interaction between condition and expression, $F(2, 36) = 5.28, p < .05$.

Figure 3 shows the mean saccade curvature in the upright condition. The eyes curved away from angry, happy, and neutral faces with mean curvature of 1.0° , 0.24° , and 0.32° , respectively. A one-way within subjects ANOVA revealed a significant effect of face, $F(2, 18) = 7.24, p < .05$. Planned comparisons revealed that curvature away from angry faces was significantly larger than curvature away from both happy, $t(9) = 3.49, p < .01$, and neutral faces, $t(9) = 4.25, p < .01$. There was no significant difference in mean curvature between neutral and happy faces, $t(9) = 0.25, p = .75$. Moreover, curvature away from angry faces was significantly different from zero, $t(9) = 3.31, p < .05$. For happy, $t(9) = 0.58, p = .58$, and neutral faces, $t(9) = 0.75, p = .47$, curvature away did not differ significantly from zero.

Mean saccade latencies for trials with angry, happy, and neutral faces were 234 ms, 237 ms, and 233 ms, respectively. A one-way within-subjects

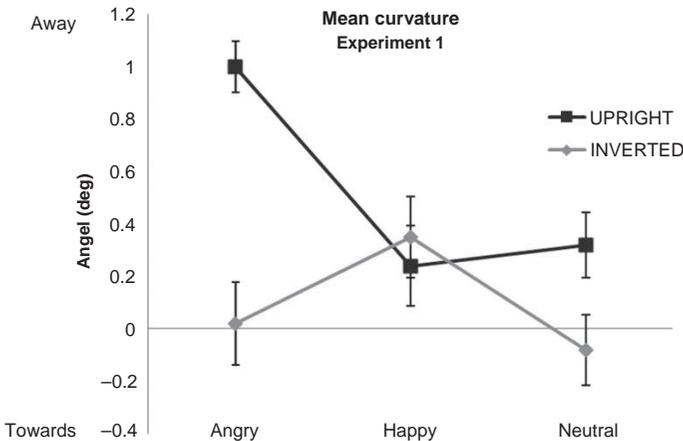


Figure 2. Mean saccade curvature averaged across participants in the upright and inverted conditions. Positive values represent deviation away from the face. Error bars reflect within-subject normalized standard errors. An interaction effect between condition and face was found.

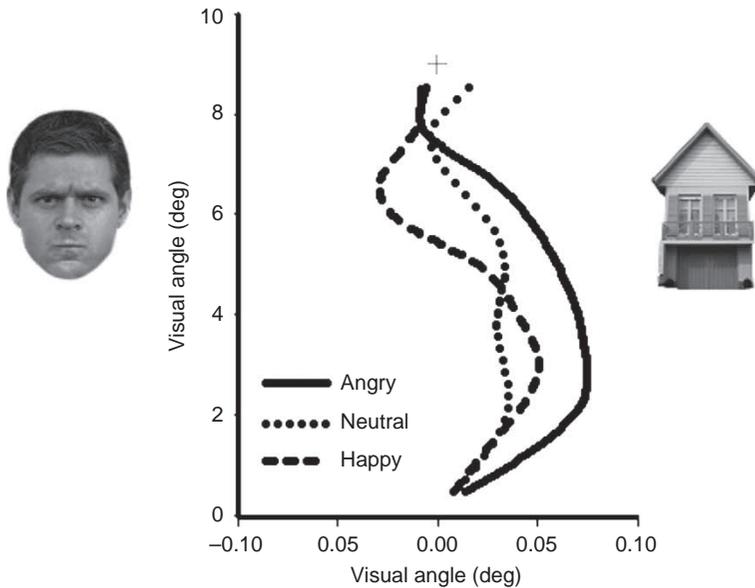


Figure 3. Saccade trajectories for angry, happy, and neutral faces averaged across participants in the upright condition. Positive values represent deviation away from the face. A significantly larger curvature away from angry faces than from neutral and happy faces was found.

ANOVA revealed no significant differences between faces, $F(2, 18) = 1.41$, $p = .27$.

Figure 4 shows the mean saccade curvatures in the inverted condition. The mean curvature for angry, happy, and neutral faces was 0.02° , 0.35° , and -0.08° , respectively. A one-way within subjects ANOVA revealed that the effect of face was not significant, $F(2, 18) = 1.02$, $p = .38$. Moreover, in contrast to the upright condition, none of the mean curvatures were significantly different from zero: Angry, $t(9) = 0.39$, $p = .71$; happy, $t(9) = 1.59$, $p = .13$; neutral, $t(9) = 0.36$, $p = .73$.

Mean saccade latencies for trials with inverted angry, happy, and neutral faces were 233 ms, 232 ms, and 229 ms, respectively. A one-way within-subjects ANOVA revealed no significant differences between faces, $F(2, 18) = 1.54$, $p = .24$. Moreover, mean saccade latencies did not differ between trials with upright (234 ms) and inverted faces (231 ms), $t(29) = 0.34$, $p = .74$, implying that the observed effects were not caused by response time variations (McSorley, Haggard, & Walker, 2006).

Experiment 1 shows that when an angry face and a neutral object are presented as irrelevant distractors in the periphery, saccade trajectories tend to curve away from the angry face. The presence of neutral or happy faces had no effect on saccade curvature. Importantly, inverting the faces

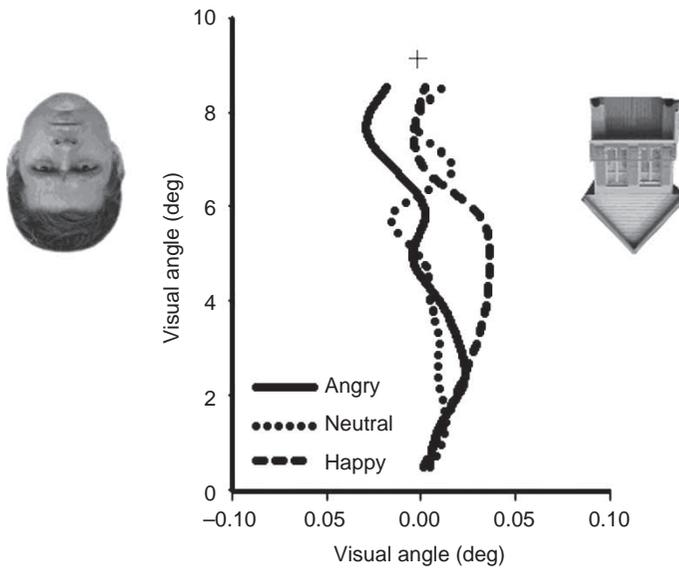


Figure 4. Saccade trajectories for angry, happy, and neutral faces averaged across participants in the inverted condition. Positive values represent deviation away from the face. No significant differences in saccade curvatures were found among emotional expressions.

eliminated the effect of the angry face on saccade curvature, suggesting that emotional expression and not the low-level features that comprise it is responsible for saccades curving away.

However, since in our task a saccade was always made to the same hemifield as the distractors, it might be argued that locations of the face and the accompanying object could have been used as a cue for the upcoming saccade target location. Note that even in this case the location of the face would still be irrelevant for determining saccade direction. However, we cannot exclude that our results are contingent upon some top-down attention being allocated to the location of both distractors, especially considering that they were the most salient objects in the display.

To make sure that distractor locations did not provide any information, in Experiment 2 we presented four objects, two in the upper and two in the lower hemifield (see Figure 5). Participants were instructed to either make a saccade to the hemifield that contained the face stimulus or to the other hemifield in which no face was presented. The location of the face (or of any of the other stimuli) was completely unpredictable of the hemifield to which one had to make a saccade. Moreover, having four objects in the visual field rather than two made it possible to determine whether the observed eye

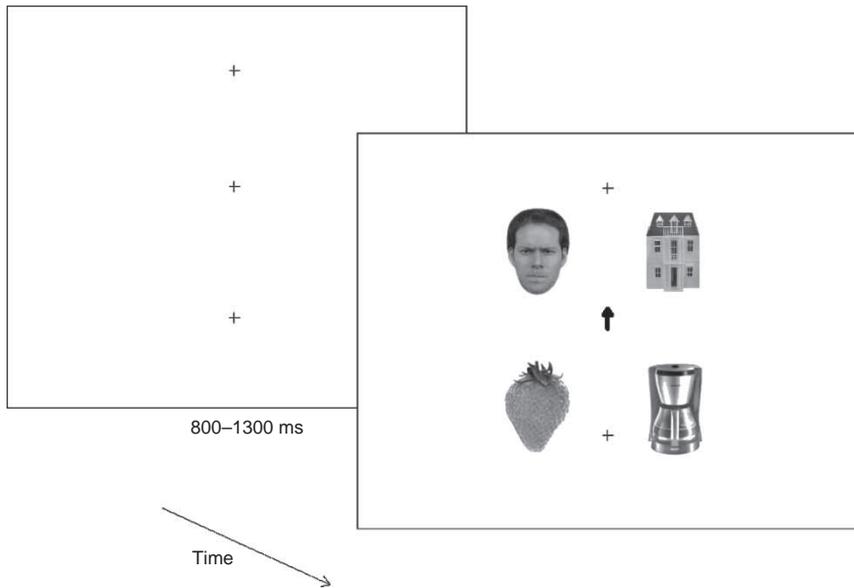


Figure 5. Schematic representation of a trial in Experiment 2. Simultaneously with presentation of an arrow, a face and three objects appeared in the periphery, at 7° from fixation.

movement effect of the presence of an angry face also holds in more cluttered environments.

EXPERIMENT 2

Method

Eight naïve students from the VU University Amsterdam (six females, mean age 23.5) participated in return for course credits or cash. All participants reported having normal or corrected-to-normal vision.

The same stimuli as in Experiment 1 were used, but rather than two pictures, four pictures (one in each quadrant) were present as distractors in the display. One of the pictures was a face with either an angry, happy, or neutral expression; the other three pictures were objects (see Figure 5). The face could appear equally likely in every quadrant. As in Experiment 1 saccades had to be made either up or down when the arrow was presented at fixation. In 50% of the trials, saccades had to be made to the same hemifield as the face. In the other 50% of the trials, saccades had to be made to the hemifield opposite to the face. The rest of the stimuli and procedure were identical to

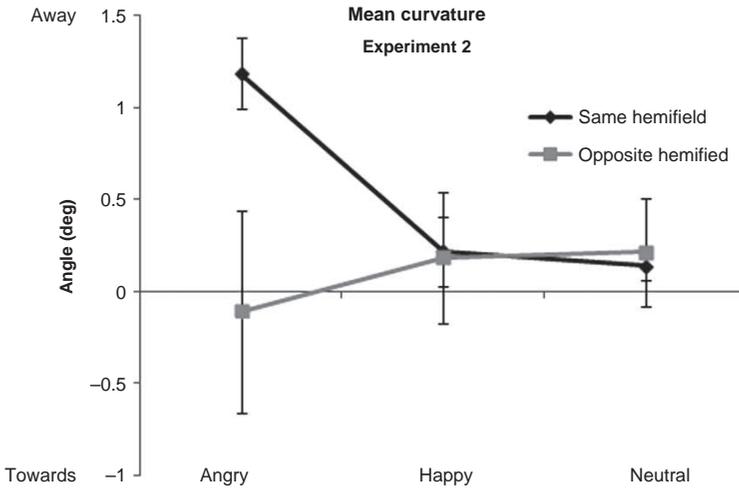


Figure 6. Mean saccade curvature averaged across participants in Experiment 2. Positive values represent deviation away from the face. Error bars reflect within-subject normalized standard errors. A main effect for face was found.

Experiment 1. The experiment started with a practice session of 24 trials and an experimental session of 768 trials.

Results and discussion

Based on the criteria described earlier, 5.5% of the trials were excluded from analyses. The number of excluded trials did not differ as a function of distractor faces.

We conducted the same analysis as in Experiment 1 examining whether the emotional expression of the face had an effect on saccade trajectories when participants made a saccade in the hemifield in which a face was present. Again as in Experiment 1, facial expression had a reliable effect on saccade curvature, $F(2, 14) = 8.59$, $p < .05$. Planned comparisons showed that curvature away from angry faces (1.18°) was significantly larger than curvature away from both happy (0.21°), $t(7) = 2.61$, $p < .05$, and neutral faces (0.14°), $t(7) = 4.54$, $p < .01$ (see Figure 6). There was no significant difference in curvature between the neutral and happy faces, $t(7) = 0.36$, $p = .73$.

Curvature away from angry faces was significantly different from zero, $t(7) = 3.73$, $p < .01$, but that was not the case for happy, $t(7) = 1.14$, $p = .29$, and neutral faces, $t(7) = 0.82$, $p = .44$. Figure 7 shows the plots of saccade trajectory averaged across participants.

For trials in which participants made a saccade in the direction opposite of the hemifield where the face was presented, there was no reliable effect of

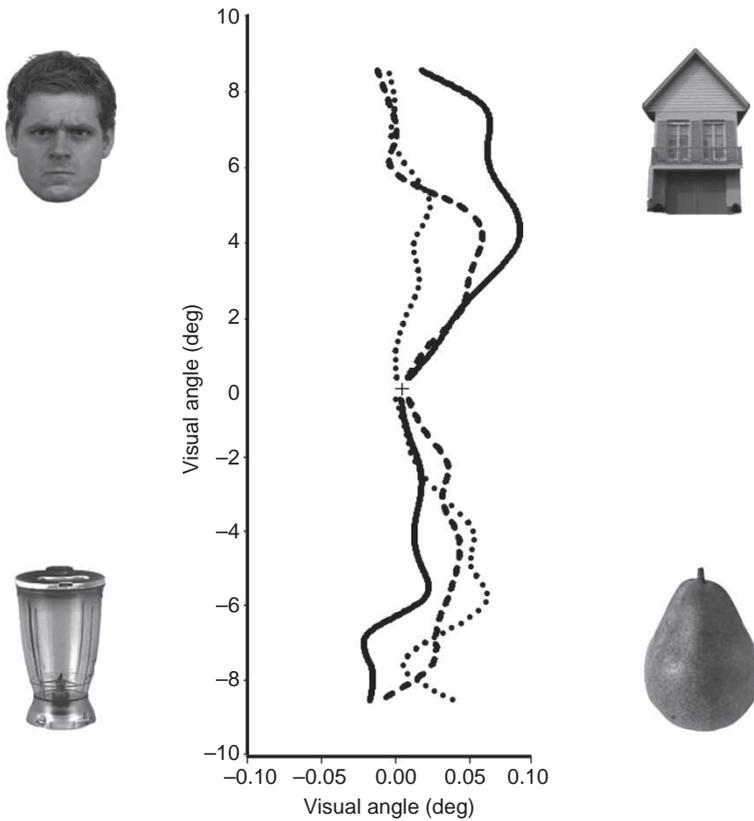


Figure 7. Saccade trajectories for angry, happy, and neutral faces averaged across participants in Experiment 2. Positive values represent deviation away from the face. For valid trials, a significantly larger curvature away from angry faces than from neutral and happy faces was found.

facial expression, $F(2, 14) = 0.12$, $p = .89$, suggesting that saccades are not affected when a face is present in the opposite hemifield as to where saccades are made.

Mean saccade latencies for trials with angry, happy and neutral faces were 259 ms, 260 ms, and 258 ms, respectively. A one-way within-subjects ANOVA revealed no significant differences between faces, $F(2, 14) = 0.135$, $p = .88$. The present results clearly show that even when the face and target hemifields are truly uncorrelated and there is no incentive to pay attention to the face, saccades curve away from angry faces, and not from happy or neutral faces. The results suggest that angry faces attract attention in a truly automatic fashion.

GENERAL DISCUSSION

The present study clearly shows that our eyes curve away from task-irrelevant angry faces presented in the periphery. Importantly, the eyes did not curve away from either neutral or happy faces, suggesting that curvature away was specific to the processing of threat and not to the general processing of faces or other emotional expressions. Mean saccade latencies did not differ among the emotional expressions, implying that the observed effects were not caused by response time variations (McSorley et al., 2006). Furthermore, in Experiment 1 there was no difference in curvature among different expressions when the faces were inverted, suggesting that the effect was not driven by low-level features, but instead by the emotional content of the face. It should be noted that there is some evidence that upright and inverted images of facial expressions of emotion are processed in a similar fashion (Calvo & Nummenmaa, 2008; Lipp, Price, & Tellegen, 2009). However, a large number of studies have also demonstrated that inversion disrupts the holistic processing of a face but maintains the low-level properties (e.g., Fox & Damjanovic, 2006; Huang, Chang, & Chen, 2011; Leder & Bruce, 2000; Tanaka & Farah, 1993). In our study, inverted faces produced no effect on saccade curvature, suggesting that emotional information was not picked up.

In Experiment 1, saccades curved away from angry faces even though the location of the face was irrelevant. It was, however, still possible that one or both stimuli would be attended to some extent, and that they could be used as an informative cue to decide where the saccade should be directed. Because there may have been some incentive to direct attention to the stimuli in the hemifield in which a saccade had to be made, the claim that the observed effect is completely stimulus driven may not be entirely justified by Experiment 1. However, in Experiment 2, we eliminated the possible involvement of top-down attention by making the face and target hemifields truly uncorrelated. Since the distractors were now present in every quadrant, the arrow was the only informative cue and the participants were therefore not required to pay attention to the any of the distractors. Similar to Experiment 1, saccades curved away from angry faces and not from happy and neutral faces, suggesting that the processing of threatening information occurred automatically.

There is some earlier evidence showing activation of the oculomotor system by pictures with an emotional content. In a study by Nummenmaa, Hyönä, and Calvo (2009), participants had to perform vertical saccades while paired emotional and neutral scenes were presented in the periphery. Results showed that both saccadic curvature and saccadic endpoint deviated away from the emotional scene. Although our results are in line with this study, there are a few important differences. First, in our study the effect

on saccade curvature was only found for a specific emotional expression (i.e., threat), whereas in Nummenmaa et al. this effect was found for all emotional expressions (i.e., both pleasant as well as unpleasant scenes). Second, in our study, saccade curvature was observed when distractors and the imperative signal to make an eye movement were presented simultaneously, implying that the expression of the face was extracted very quickly and affected the saccade trajectory very quickly. In contrast, Nummenmaa and colleagues only found curvature away when the distractor scenes were presented 150 ms before the imperative signal. Such differences in the pattern of results between the two studies was most likely due to the fact that in our experiments we used faces instead of complex emotional scenes, possibly isolating the effect of threat from the influence of high-level cognitive factors. Finally, our study included a control condition with inverted faces in which we did not see any effect on saccade trajectories, ruling out the possibility that low-level features were driving the effect.

Similarly, in a recent study Weaver, Lauwereyns, and Theeuwes (2011) showed that, relative to neutral words, the eyes curve away from irrelevant peripherally presented taboo words. This study demonstrates that even semantic word content (i.e., emotionally loaded words) may affect the oculomotor system. Note, however, that this effect occurred much later. To see an effect on saccade curvature, the word had to be presented 800 ms before the saccade was launched. At shorter SOAs the content of the word had no effect on saccade curvature.

Saccade curvature has usually been attributed to competition for potential saccade targets in the oculomotor map, which is presumably located in the intermediate layers of the superior colliculus (Sparks & Hartwich-Young, 1989). The ultimate direction of a saccade is determined by the mean vector of simultaneously active, but spatially separated populations of neurons corresponding to different locations of activity in the oculomotor map (Lee, Rohrer, & Sparks, 1988). When a saccade is initiated to a target location, the location of a salient distractor needs to be suppressed to allow an accurate eye movement to the saccade goal. This suppression leads to a shift in the mean vector of activity, resulting in the eye movement deviating away from the salient stimulus (Doyle & Walker, 2001; Godijn & Theeuwes, 2002). For example, curvature away has been demonstrated for exogenously and endogenously covertly attended locations (Rizzolatti et al., 1987; Sheliga et al., 1994) and locations maintained in working memory (Belopolsky & Theeuwes, 2011; Theeuwes, Olivers, & Chizk, 2005; Theeuwes, Van der Stigchel, & Olivers, 2006).

Just as the automatic allocation of attention to a salient distractor results in a strong activation of the oculomotor system (Ludwig & Gilchrist, 2003), our results suggest that an irrelevant angry face is treated as a salient stimulus and can generate competition within the oculomotor system. In contrast,

no modulation of saccade trajectory by faces with other expressions was observed, suggesting that these types of faces are not as salient for the oculomotor system as the threatening faces. Our results extend the earlier studies by showing that threat is processed automatically and is biasing our overt behaviour. The biological relevance of such automatic allocation of attention to irrelevant threatening stimuli is evident, since it can help an organism to quickly and efficiently localize and respond to threat.

The neural mechanisms underlying the prioritized processing of threat are still highly debated (de Gelder, van Honk, & Tamietto, 2011; Pessoa & Adolphs, 2011). A large number of studies suggested that a direct subcortical route, via the superior colliculus (SC) to the amygdala, is involved in fast processing of threat. As the SC is important structure in the generation of saccadic eye movements, it may represent a key neural candidate to organize a rapid integration between emotional input and oculomotor output processes. In line with this view, our study provides evidence for a rapid coding of threat in the oculomotor system. In the present study, SC activity caused by the threatening face was present near the moment that a saccade to the target had to be made, and therefore needed to be inhibited causing the saccade to curve away from the threatening face. A peak of activation in the oculomotor map of the SC caused by an angry face required inhibition of that location, causing the eyes to curve away from the angry face.

In summary, the present study clearly showed that saccades curved away from irrelevant angry faces. We propose that such curvature away reflects automatic allocation of attention to threat which in turn generates activity in the oculomotor system. Thus, in addition to stimuli that are salient because of their physical features or sudden onset, the threatening content of a face is automatically prioritized in the oculomotor system and biases behaviour.

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