attention with saccades

Rachel L. Bannerman

Vision Research Laboratories, School of Psychology, University of Aberdeen, Aberdeen, United Kingdom

Vision Research Laboratories, School of Psychology, University of Aberdeen, Aberdeen, United Kingdom



ᡣᠠᡝᢦ᠌

 $\square \square$

Vision Research Laboratories, School of Psychology, University of Aberdeen, Aberdeen, United Kingdom



Arash Sahraie

Maarten Milders

According to theories of attention and emotion, threat-related stimuli (e.g., negative facial expressions) capture and hold attention. Despite these theories, previous examination of attentional cueing by threat showed no enhanced capture at brief durations. One explanation for the absence of attentional capture effects may be related to the sensitivity of the manual response measure employed. Here we extended beyond facial expressions and investigated the time course of orienting attention towards fearful body postures in the exogenous cueing task. Cue duration (20, 40, 60, or 100 ms), orientation (upright or inverted), and response mode (saccadic eye movement or manual keypress) were manipulated across three experiments. In the saccade mode, both enhanced attentional capture and impaired disengagement from fearful bodies were evident and limited to rapid cue durations (20 and 40 ms), suggesting that saccadic cueing effects emerge rapidly and are short lived. In the manual mode, fearful bodies impacted only upon the disengagement component of attention at 100 ms, suggesting that manual cueing effects emerge over longer periods of time. No cueing modulation was found for inverted presentation, suggesting that valence, not low-level image confounds, was responsible for the cueing effects. Importantly, saccades could reveal threat biases at brief cue durations consistent with current theories of emotion and attention.

Keywords: saccades, emotion, body postures, attention

Citation: Bannerman, R. L., Milders, M., & Sahraie, A. (2010). Attentional cueing: Fearful body postures capture attention with saccades. *Journal of Vision*, *10*(5):23, 1–14, http://journalofvision.org/content/10/5/23, doi:10.1167/10.5.23.

Introduction

Theories of emotion and attention propose that a predisposition to orient very rapidly towards signals of threat is evident in all of us, acting as a self-preservation mechanism, critical for survival (Le Doux, 1996; Mathews & Mackintosh, 1998; Öhman & Mineka, 2001). As such, it has been argued that threat-related stimuli have a special propensity to attract an observer's attention. A number of cognitive-experimental tasks have been employed to investigate this proposal. In particular, studies using the visual search (Fox et al., 2000; Lundqvist & Öhman, 2005; Öhman, Lundqvist, & Esteves, 2001) and dot-probe (Bradley, Mogg, Falla, & Hamilton, 1998; Bradley, Mogg, & Millar, 2000; Mogg & Bradley, 1999) tasks have provided evidence that threat-related stimuli are processed in a preferential manner. In the visual search task, participants are required to search for a target stimulus embedded in an array of distracters. Using this task, a number of studies have demonstrated faster reaction times

for detection of targets which are threat-related compared to those which are non-threatening (Fox et al., 2000; Lundqvist & Öhman, 2005; Öhman et al., 2001). In the dot-probe task, two images are presented simultaneously followed by the appearance of a dot probe in one of the two image locations. Participants press a button as soon as they detect the dot. Several studies have shown that participants respond faster when the dot replaces a threatrelated compared to non-threatening stimulus (Bradley et al., 1998, 2000; Mogg & Bradley, 1999).

Despite the abundant behavioral evidence gained from visual search and dot-probe tasks, both of these tasks are subject to interpretation problems. Notably, the simultaneous presentation of threat-related and neutral stimuli makes it difficult to ascertain whether threat-related stimuli draw attentional resources towards themselves from the outset or whether once a threat-related stimulus has been detected attention tends to reside in that location making disengagement from threat difficult (Fox, Russo, Bowles, & Dutton, 2001). The specific constitutes of the attentional bias towards threat-related stimuli is at present

doi: 10.1167/10.5.23

Downloaded from jov.arvojournals.org on 06/29/2019

the subject of ongoing debate. Attending to a new stimulus is thought to comprise three components: (a) the initial orienting of attention towards the stimulus, (b) engaging attention with the stimulus, and (c) disengaging attention from the stimulus (Posner, 1980). The first two components are related to attentional capture by threat, while the third is related to increased difficulties in shifting attention away from threat. It has been suggested that attentional capture is an encapsulated process (Fox et al., 2001), meaning that it is relatively impenetrable to cognitive control and unaffected by emotional meaning. This surprising postulation runs counter to theories (Le Doux, 1996; Mathews & Mackintosh, 1998; Öhman & Mineka, 2001) that propose a quick orientation of attention to threatening stimuli, resulting in improved awareness of threat in the environment. Impaired attentional disengagement may be related to difficulties in task performance in the presence of threat (Koster, Crombez, Verschuere, Van Damme, & Wiersema, 2006).

The ability of threat-related stimuli to modulate the capture and disengagement components of attention, thereby circumventing the interpretational problems of the dot-probe task, can be measured using the exogenous cueing paradigm. In its original form (Posner, 1980), a cue stimulus is presented in the left or right hemifield and a target is presented in the same (valid) or opposite (invalid) spatial location where the cue had appeared. Faster reaction times for the target in valid trials are thought to reflect attentional capture by the cue, whereas slower reaction times in invalid trials are thought to indicate difficulty in disengaging attention from the cue. In the emotional modification of the exogenous cueing paradigm, the emotional meaning (e.g., threat-related, neutral) of the cue is manipulated enabling an investigation into attentional capture and disengagement as a function of cue valence. A number of studies have investigated attentional cueing by threat with inconsistent findings. For example, difficulty in disengaging attention from threat has been demonstrated by slower responses on invalid trials containing threat-related cues compared to invalid trials containing neutral cues (Fox et al., 2001; Fox, Russo, & Dutton, 2002; Yiend & Mathews, 2001). Disengagement effects have been found for threat-related words (Fox et al., 2001), facial expressions (Fox et al., 2002), and natural scenes (Yiend & Mathews, 2001), with such effects appearing to be restricted to highly anxious individuals. Alternatively, other studies have demonstrated attentional capture by threat, as evidenced by faster responses on valid trials containing threat-related cues compared to valid trials containing neutral cues (Koster, Crombez, Van Damme, Verschuere, & De Houwer, 2004; Koster, Crombez, Verschuere, Vanvolsem, & De Houwer, 2007). Interestingly, attentional capture effects have been observed with threat-related natural scenes (Koster et al., 2007) and aversively conditioned cues (Koster et al., 2004) in studies not selecting for high levels of anxiety.

Importantly, most emotional exogenous cueing tasks have used manual responses and relatively long cue durations. Long cue durations (e.g., 500 ms) allow for more detailed processing and therefore have been shown to be involved in sustaining attention (e.g., delayed disengagement) but not capture by threat (Yiend & Mathews, 2001). Conversely, shorter cue durations (e.g., 100-300 ms) produce mixed results with some studies showing both capture and disengagement effects in anxious (Koster et al., 2006) and normal (Koster et al., 2004) individuals, while in other studies only disengagement effects have been found (Fox et al., 2001, 2002). However, current emotion theories (Le Doux, 1996; Mathews & Mackintosh, 1998; Öhman & Mineka, 2001) posit that fast attentional orienting towards threat is most adaptive immediately after its presentation. Therefore, based on theory, one would assume that at rapid cue durations the attentional capture component should be modulated by threat. Despite this, a recent study which employed rapid cue duration (e.g., 28 ms) failed to find either enhanced attentional capture or difficulty in disengaging attention from threat-related scenes (Koster et al., 2007). The lack of facilitated capture at brief cue durations has been interpreted as short cue presentation being insufficient to extract the threatening nature of the stimulus. However, this is discrepant to findings which have shown that the amygdala responds to masked threatrelated faces presented briefly (Pessoa, McKenna, Gutierrez, & Ungerleider, 2002) and early electrophysiological markers react to threat-related expressions after short presentation (Fox, Derakshan, & Shoker, 2008). Most importantly, the encapsulation and associated absence of enhanced capture by threat at brief presentations does not fit with current theories (Le Doux, 1996; Mathews & Mackintosh, 1998; Öhman & Mineka, 2001) that propose a fast orientation of attention towards threat, even when the threat is presented briefly.

One plausible explanation for the lack of facilitated capture at brief durations may be related to the sensitivity of the manual response measure employed. In terms of assessing valence, a parsimonious model would imply that both manual and saccadic responses access a unified mechanism in a similar fashion. Alternatively, the response parameter of interest may change when different response modes and stimulus durations are used in an attentional manipulation task. Recent studies have shown that there are differences in manual and saccadic responses for detection of briefly presented threat-related and neutral stimuli (Bannerman, Milders, de Gelder, & Sahraie, 2009; Bannerman, Milders, & Sahraie, 2009). Notably, saccadic biases towards threat (i.e., faster detection of fearful compared to neutral stimuli) emerged at very brief stimulus durations (20 ms), whereas manual threat-related biases emerged only at longer (500 ms) stimulus durations, suggesting that saccades are sensitive to threat at shorter stimulus durations. These findings can be related to the relative speed of saccades which means that they are initiated on the basis of less information than manual hand movements, suggesting that they can reveal earlier stages of processing than manual responses (Hunt, van Zoest, & Kingstone, 2010).

Although several studies have examined saccades towards threat-related and neutral stimuli (Hermans, Vansteenwegen, & Eelen, 1999; Hunt, Cooper, Hungr, & Kingstone, 2007; Kissler & Keil, 2008; Nummenmaa, Hyöna, & Calvo, 2006), these studies did not directly compare saccadic and manual responses. Moreover, with the exception of one study (Kissler & Keil, 2008), threatrelated and neutral stimuli were presented simultaneously, making it difficult to isolate the capture and disengagement components of attention. Given the rapid and naturalistic nature of saccades, it would not be surprising to find that they can provide an ideal tool for examining attentional capture and that this capture may become modulated by emotional meaning. This would run counter to the assumption, gained from emotional exogenous cueing studies using manual responses, that the attentional capture component is an encapsulated process, unaffected by emotional meaning (Fox et al., 2001).

In addition, the stimuli employed in most behavioral studies investigating attention towards threat to date has consisted mainly of negative facial expressions, pictures of aversive scenes, and aversive words. Recently, however, research has started to extend beyond facial expressions and investigate the importance of perceiving emotional body language. This work has shown that emotional body stimuli can be easily recognized even when no verbal labels are provided (Van den Stock, Righart, & de Gelder, 2007). Moreover, there are intriguing similarities in the way we process faces and bodies. For example, it is claimed that faces are processed holistically as indicated by the inversion effect (holistic stimuli presented upside down are more difficult to recognize than other inverted stimuli) (Tanaka & Farah, 1993). More recently, this effect has been documented for bodies with recognition of body stimuli being more impaired by inversion than the recognition of houses (Reed, Stone, Bozova, & Tanaka, 2003). Interestingly, when faces and bodies are compared directly, the magnitude of the inversion effect is similar, with comparable error rates in recognizing both types of inverted stimuli (Reed et al., 2003). Furthermore, both behavioral face and body inversion effects appear to be mediated by face-selective brain regions such as the fusiform face area (FFA) (Brandman & Yovel, 2010; Yovel & Kanwisher, 2005). Notably, the FFA shows adaptation effects (e.g., greater response for same body posture pairs compared to different body posture pairs) for upright but not inverted bodies, suggesting that the body inversion effect is mediated by face processing mechanisms (Brandman & Yovel, 2010). Akin to these functional brain imaging findings observed with upright and inverted neutral faces and body postures, Hadjikhani and de Gelder (2003) have

shown that viewing fearful bodily expressions activates the fusiform gyrus and the amygdala, two brain areas associated with the processing of faces and facial expressions (Kanwisher, McDermott, & Chun, 1997; Morris et al., 1998). In addition to behavioral and functional brain imaging findings, EEG has shown that body images, like faces, have been found to elicit the N170 component (Meeren, van Heijnsbergen, & de Gelder, 2005), suggesting that the initial stages of face and body processing are probably similar. Moreover, the perception of fear in faces and bodies appears to be similar, with EEG findings also showing that viewing fearful compared to neutral bodily expressions produces an early emotion effect on the P1 component with faster latencies for fearful bodies compared to neutral bodies (van Heijnsbergen, Meeren, Grezes, & de Gelder, 2007), thus far only documented for fearful faces (Righart & de Gelder, 2006).

In the current study, we investigated attentional cueing by peripherally presented threat-related stimuli. We extended findings beyond facial expressions and utilized threat-related body postures to investigate whether fear conveyed through body postures could modulate the capture and disengagement components of attention. In addition, we systematically varied the response mode (saccadic response vs. manual response) and duration (20 and 100 ms: Experiments 1 and 2) (20, 40, 60, and 100 ms: Experiment 3) of the cue to elucidate the time course of threat-related attentional cueing by different response systems. It was predicted that threat-related body postures would be sufficiently salient to modulate attention, thus showing that fear conveyed through body postures can act as a signal of danger. Moreover, based on previous examinations (Bannerman, Milders, de Gelder, et al., 2009; Bannerman, Milders, & Sahraie, 2009), it was hypothesized that the time course of threatrelated biases would show divergence for difference response modes, with saccades showing threat-related cueing effects at short durations and manual responses showing threat biases at longer durations. Most importantly, given the overt nature of saccades, it was further predicted that the attentional capture component would become modulated by threat when examined via eye movements but not manual responses. This would show that the attentional capture component is not, as previously thought, an encapsulated process.

Experiment 1: Cueing with fearful and neutral body postures

Methods

Participants

Twenty participants (10 female and 10 male; mean age = 21.8 years; range = 18-26 years) took part. All had normal visual acuity and normal state (M = 32.3, SD = 7) and trait

3



Figure 1. Schematic representation of presentation sequence. After a 1000-ms fixation episode, a time gap (blank screen) for 200 ms preceded the presentation of a fearful or neutral body posture on the left or right side of the screen for either 20 or 100 ms. This was followed by the appearance of the target (+) for 1000 ms in either the same (valid trial) or opposite (invalid trial) spatial location to the cue.

(M = 32.8, SD = 8) anxiety levels as measured by the State Trait Anxiety Inventory (STAI; Spielberger, Gorsuch, Lushene, Vagg, & Jacobs, 1983).

Materials and procedure

The stimuli consisted of body images of 10 individuals (with the face blurred), 5 male and 5 female, taken from a standard set of body expression pictures (see Van den Stock et al., 2007). In the body pictures, each individual performed meaningful actions that expressed fear or were emotionally neutral (e.g., pouring juice into a glass, combing their hair, speaking on the phone). These whole neutral body actions provide a suitable control because similar to emotional body actions, they contain the illusion of biological movements, have semantic properties, and they are familiar (de Gelder, Snyder, Greve, Gerard, & Hadjikhani, 2004). The body images subtended on average $6.8^{\circ} \times 17.0^{\circ}$, at a viewing distance of 37 cm (as used in previous investigation; Bannerman, Milders, de Gelder, et al., 2009; Bannerman, Milders, & Sahraie, 2009), and were used as cues in the experiment. The target that participants had to localize was a fixation cross, which subtended $1.5^{\circ} \times 1.5^{\circ}$. Both cue and target stimuli were presented against a uniform white background and were positioned to the left and right of a fixation cross, centered at 9.2° eccentricity. All stimuli were presented on a 21-inch CRT monitor with 100-Hz refresh rate using a SVGA graphics card (Cambridge Research Systems, UK) in a dimly lit room (10 lx).

For the saccade mode, the sequence of events within each trial was as follows. A fixation point appeared in the center of the screen for 1000 ms, followed by a 200-ms gap period (blank screen), thought to speed up saccade initiation (Fischer & Weber, 1993; Saslow, 1967). A body cue (fearful or neutral) was then presented on the left or right side of the screen for either 20 or 100 ms. The target (+) was presented immediately after on the left or right side of the screen for 1000 ms (see Figure 1). The participants' task was to saccade, as quickly as possible, towards the target. A fixation at the target was defined as the moment a saccade penetrated the region at which the target cross was situated. For the saccade mode, each participant performed 320 trials, divided into 8 blocks of 40 trials each (4 blocks at 20-ms cue duration; 4 blocks at 100-ms cue duration). Block order was randomized between participants. Within each block of trials, 20 trials were valid (i.e., the cue and target appeared in the same spatial location) and 20 trials were invalid (i.e., the cue and target appeared in opposite spatial locations). The trials were presented in a different randomized order for each participant. This resulted in 50% (160) of the experimental trials being valid and 50% (160) being invalid overall. Participants were informed that the body cue would predict the location of the target on some, but not all of the trials. The experimental protocol for the manual mode was exactly the same as those for the saccade mode except that participants had to indicate the location of the target by manually pressing one of two buttons on a response box as quickly and accurately as possible. The ordering of the response mode (saccade and manual) was counterbalanced between participants.

Response recording

Eye movements were monitored and recorded using electro-oculography (EOG). Horizontal eye movements were recorded using 4-mm electrodes applied to the



Figure 2. Example of eye trace showing a correct saccade to the right, following a fearful body cue presented for 20 ms, with a reaction time of 125 ms. Amplitude thresholds (30 mV) are indicated by black horizontal lines. Only saccades that crossed these thresholds were analyzed. Saccadic reaction time (SRT) was determined as the time difference between the offset of the cue stimulus (Time 0) and the start of the saccade towards the target cross. Saccadic onset time was recorded at 10% change in amplitude between steady fixation and final landing position (black circle). Once making the saccade to the target cross, the participant moves their eyes back to the center of the screen prior to the next trial.

participants' left and right canthi and ear (ground), employing the DC method and a sampling rate of 1000 Hz (ACKNOWLEGDE v. 3.59: Biopac Systems). Head position was stabilized via a forehead and chin rest. Saccadic reaction time (SRT) was determined as the time difference between the offset of the cue stimulus (time 0) and the start of the saccade towards the target stimulus. As a first criterion, only saccades on correct trials and that exceeded an amplitude threshold of greater than 30 mV were analyzed (saccade detection criterion). As a second criterion, saccadic onset was recorded at a 10% change in amplitude between steady fixation and final landing position. This was equivalent to 1.3° deviation from fixation (see Figure 2). Each trial was verified independently by the experimenter to make sure that these criterions were met. This two stage process eliminates artifacts due to drift in central position in the absence of a saccade and has been reported previously to be a good alternative to the velocity profile approach (Bannerman, Milders, de Gelder, et al., 2009; Bannerman, Milders, &

Sahraie, 2009). SRTs faster than 80 ms were discarded on the basis that these saccades may be anticipatory and result in chance performance (Kaylesnykas & Hallett, 1987). In both the saccade and manual modes, RTs more than 3 *SD* above the mean were also discarded. Consequently, of the original 320 saccadic and 320 manual trials per participant, on average 7.4% were rejected.

Results and discussion

Mean reaction times (RTs) are displayed in Figures 3A (saccade mode) and 3B (manual mode). Mean correct RTs were analyzed by a 2 (mode: saccadic vs. manual response) × 2 (cue duration: 20 ms. vs. 100 ms) × 2 (cue valence: fearful vs. neutral) × 2 (cue validity: valid vs. invalid) ANOVA. There were main effects for mode, F(1, 19) = 76.53, MSE = 1631633, p < 0.001, $\eta_p^2 = .80$, cue duration, F(1, 19) = 6.02, MSE = 25347, p < 0.05,



Figure 3. Mean saccadic and manual reaction times for valid/invalid fearful and neutral cue trials in Experiment 1 (A and B). Mean saccadic and manual reaction times for valid/invalid upright and inverted fearful cue trials in Experiment 2 (C and D). Error bars represent standard errors of the mean (*SEM*).

 $\eta_p^2 = .24$, and cue validity, F(1, 19) = 27.57, MSE = 17199, p < 0.001, $\eta_p^2 = .59$. Participants were faster overall in the saccade (M = 233 ms, SD = 19) compared to manual (M = 378 ms, SD = 66) mode (p < 0.001); at 20-ms (M = 295 ms, SD = 39) compared to 100-ms (M = 313 ms, SD = 32) cue duration (p < 0.05); and when the target was valid (M = 297 ms, SD = 32) compared to invalid (M = 311 ms, SD = 33) (p < 0.001), respectively. Importantly, there was a significant four-way interaction between Mode × Cue Duration × Cue Valence × Cue Validity, F(1, 19) = 9.94, MSE = 5281, p < 0.01, $\eta_p^2 = .34$. To interpret the four-way interaction, separate ANOVAs were conducted for each response mode.

Saccade mode

In the saccade mode, a 2 (cue duration: 20 ms. vs. 100 ms) \times 2 (cue valence: fearful vs. neutral) \times 2 (cue validity: valid vs. invalid) ANOVA showed significant

main effects of cue duration, F(1, 19) = 54.40, MSE = 111514, p < 0.001, $\eta_p^2 = .74$, with faster SRTs at 20 ms (M = 206 ms, SD = 18) compared to 100 ms (M = 259 ms, SD = 30), and cue validity, F(1, 19) = 20.47, MSE = 10498, p < 0.001, $\eta_p^2 = .52$, with faster SRTs on valid (M = 225 ms, SD = 25) compared to invalid (M = 241 ms, SD = 15) trials. The interaction between Cue Duration × Cue Valence × Cue Validity was also significant, F(1, 19) = 7.38, MSE = 1416, p < 0.05, $\eta_p^2 = .28$. To interpret this interaction, separate 2 (cue valence) × 2 (cue validity) ANOVAs were performed at each cue duration.

At 20-ms cue duration, there was a significant main effect of cue validity, F(1, 19) = 17.28, MSE = 3976, p < 0.01, $\eta_p^2 = .48$, with faster SRTs on valid (M = 199 ms, SD = 17) compared to invalid (M = 213 ms, SD = 22) trials. More importantly, a significant interaction between Cue Valence × Cue Validity, F(1, 19) = 13.17, MSE = 2040, p < 0.01, $\eta_p^2 = .41$, was observed. To examine this interaction, further paired samples *t* tests were conducted

7

to assess attentional capture and disengagement effects. Emotional effect on attentional capture was investigated by comparing the mean SRT for fearful and neutral body cues on valid cue trials. At 20-ms cue duration, SRTs following valid fearful body cues (M = 193 ms, SD = 17) were faster than SRTs following valid neutral body cues (M = 206 ms, SD = 20) [t(19) = 3.18, p < 0.01], indicative of facilitated attentional capture by fearful body postures. Emotional effect on attentional disengagement was assessed by comparing the mean SRT for fearful and neutral body cues on invalid cue trials. At 20-ms cue duration, SRTs following invalid fearful body cues (M =217 ms, SD = 23) were slower than SRTs following invalid neutral body cues (M = 210 ms, SD = 22) [t(19) =2.82, p < 0.01], indicative of difficulty in disengaging attention from fearful bodies. Formal statistical analysis of accuracy levels (percentage of correct eye movements towards the target) was consistent with this view in that accuracy levels were significantly lower on invalid trials when the body cue was fearful (M = 71.8%, SD = 6)compared to neutral (M = 80.3%, SD = 5) [t(19) = 6.95, p < 0.001].

At 100-ms cue duration, the 2 (cue valence) \times 2 (cue validity) ANOVA, revealed a significant main effect of cue validity, F(1, 19) = 8.60, MSE = 6698, p < 0.01, $\eta_p^2 = .31$, with faster SRTs on valid (M = 250 ms, SD = 41) compared to invalid (M = 268 ms, SD = 24) trials, but no Cue Valence \times Cue Validity Interaction, F(1, 19) = 0.28, MSE = 65, p > .6, $\eta_p^2 = .01$. At 100-ms cue duration, there were no significant differences in SRT between fearful and neutral bodies on valid [t(19) = 0.19, p = .849] or invalid [t(19) = 1.35, p = .193] trials and no significant differences in the accuracy of responses [t(19) = 1.17, p = .255] between fear and neutral on invalid trials. No enhanced attentional capture by, or delayed disengagement from, fearful body postures was observed at 100-ms cue duration in the saccade mode.

Manual mode

In the manual mode, a 2 (cue duration: 20 ms. vs. 100 ms) × 2 (cue valence: fearful vs. neutral) × 2 (cue validity: valid vs. invalid) ANOVA showed a significant main effect of cue validity, F(1, 19) = 14.68, MSE = 6891, p < 0.01, $\eta_p^2 = .44$, with faster manual reaction times (MRTs) on valid (M = 369 ms, SD = 64) compared to invalid (M = 382 ms, SD = 68) trials, and a significant three-way interaction between Cue Duration × Cue Valence × Cue Validity, F(1, 19) = 5.65, MSE = 4244, p < 0.05, $\eta_p^2 = .23$.

A 2 (cue valence) × 2 (cue validity) ANOVA at 20-ms cue duration showed a main effect of cue validity, F(1, 19) = 4.37, MSE = 2174, p < 0.05, $\eta_p^2 = .19$. MRTs were faster on valid (M = 379 ms, SD = 78) compared to invalid (M = 389 ms, SD = 75) trials. However, there was no significant interaction between Cue Valence × Cue Validity, F(1, 19) = 2.23, MSE = 1240, p > .2, $\eta_p^2 = .11$. At

20-ms cue duration, there were no significant differences in MRT between fearful and neutral bodies on valid [t(19)= 0.59, p = .559] or invalid [t(19) = 1.54, p = .139] trials and no significant differences in the accuracy of responses [t(19) = 1.05, p = .308] between fear and neutral on invalid trials, indicating no enhanced attentional capture by, or delayed disengagement from, fearful body postures.

A 2 (cue valence) \times 2 (cue validity) ANOVA at 100-ms cue duration revealed a significant main effect of cue validity, F(1, 19) = 8.35, MSE = 5009, p < 0.01, $\eta_p^2 = .31$, with faster MRTs on valid (M = 359 ms, SD = 59) compared to invalid (M = 375 ms, SD = 64) trials. The Cue Valence \times Cue Validity interaction was marginally significant, F(1, 19) = 3.56, MSE = 3239, p = .075, $\eta_p^2 =$.16. Paired samples t tests showed no significant differences in MRT between fearful and neutral bodies on valid trials [t(19) = 0.59, p = .559], indicating no enhanced attentional capture by fearful body postures. However, on invalid trials, there was a trend towards slower MRTs following fearful bodies (M = 384 ms, SD = 73) compared to neutral bodies (M = 366 ms, SD = 63) [t(19) = 1.89, p =.074], showing that difficulty in disengaging attention from fearful bodies was evident only marginally at 100 ms. However, unlike the saccade mode, there were no significant differences in the accuracy of responses [t(19) = 0.85,p = .853] between fear and neutral on invalid trials.

In summary, Experiment 1 showed divergence of the time course for saccadic and manual cueing responses. Notably, in the saccade mode, both enhanced capture and slower disengagement of attention from fearful bodies was observed at 20-ms cue duration. This effect appeared to be a short-lived phenomenon as no facilitated attentional capture or impaired disengagement from fearful bodies was observed at 100-ms cue duration in the saccade mode. Conversely, in the manual mode, no cueing effects (capture or disengagement) were observed at 20-ms cue duration. However, when the body cues were presented for 100 ms, the valence of the body cue did affect manual reaction times, but this effect was evident only marginally in the disengagement component of attention.

Despite the cueing effects observed, it is possible that saccadic and manual RTs were not influenced by the emotional content of the body cues but simply by low-level image differences between fearful and neutral bodies. While fearful body postures lack the salient features of fearful faces, like wide eye whites, they may contain other salient aspects that could also generate fast reaction times. We examined this issue using three main strategies.

Further analysis/control experiment Attentional capture and disengagement effects with specific images

Firstly, if the results are based mainly on the level of fear expressed by the body postures, then it would be reasonable to assume that breaking the image set down according to the perceived intensity of fear and neutral and comparing the responses of the most fearful postures to those of neutral would enhance the cueing modulation. Based on previous investigation using the same body postures (Bannerman, Milders, de Gelder, et al., 2009), we had ratings of the emotional intensity of each body posture on a 5-point Likert scale, ranging from 1 = not at all intense to 5 = extremely intense. The ratings data showed that fearful body postures (M = 3.4, SD = 0.5) were rated as more emotionally intense than neutral body postures (M =2.9, SD = .3) [t(9) = 3.42, p < 0.01]. Moreover, three fearful postures were consistently rated as more emotionally intense (M = 4.0, 4.5, and 4.6, respectively) than the remaining seven postures (range = 3.0-3.7).

Analysis using the three most fearful body postures and comparing these to the neutral body postures enhanced both saccadic and manual cueing effects at the respective durations shown in Experiment 1 (i.e., 20 ms in the saccade mode, 100 ms in the manual mode). Notably, on valid trials, in the saccade mode, participants initiated a saccade to a target preceded by the most fearful body cues with a mean SRT of 189 ms and to a target preceded by the least fearful body cues with a mean SRT of 197 ms. The SRT benefit of a fearful cue compared to neutral cue on valid trials was significantly larger for the most fearful body cues (M = 17 ms, SD = 21) compared to the least fearful body cues (M = 9 ms, SD = 18) [t(19) = 3.23, p < 1000.01]. On invalid trials, participants initiated a saccade to a target preceded by the most fearful body cues with a mean SRT of 222 ms and to a target preceded by the least fearful body cues with a mean SRT of 211 ms. The SRT cost of a fearful compared to neutral cue on invalid trials was marginally significantly larger for the most fearful body cues (M = 12 ms, SD = 18) compared to the least fearful body cues (M = 2 ms, SD = 13) [t(19) = 2.08, p =.052]. In the manual mode, the most fearful body postures led to an enhancement of the disengagement effect. Notably, on invalid trials, participants detected a target preceded by the most fearful body cues with a mean MRT of 393 ms and the least fearful with a mean MRT of 375 ms. The MRT cost of a fearful compared to neutral cue on invalid trials was significantly larger for the most fearful body cues (M = 27 ms, SD = 41) compared to the least fearful body cues (M = 10 ms, SD = 41) [t(19) = 11.62,p < .001]. Therefore, breaking the image set down according to perceived intensity of fear and neutral suggests that the SRT benefit and cost, and MRT cost, of fearful cues are based on the level of fear expressed by the images.

Saccadic baseline

To further examine whether the cueing effects were due to valence or low level image differences, 10 participants (5 female and 5 male; mean age = 20.9 years; range = 19-24 years) who participated in Experiment 1 performed a saccadic baseline task in which a single fearful or neutral body posture was presented for 20 or 100 ms in the left or right visual field. Participants were asked to saccade towards the image as quickly as possible. It was checked that participants always fixated the center of the screen prior to each trial. Any trials where participants were not fixated centrally were removed (approximately 2.0% of overall trials). The mean reaction times for both fearful and neutral targets were similar to human express saccades (120 ms; Fischer & Weber, 1993), with saccades to fearful postures (M = 121, SD = 26) being initiated faster than saccades to neutral postures (M = 164, SD = 30) at 20 ms stimulus duration [t(9) = 5.32, p < 0.001] but not at 100 ms stimulus duration (fearful posture: M = 138, SD = 23; neutral posture: M = 150, SD = 18; p = .174).

To control for the attractiveness of each body cue, we subtracted the mean SRTs for the fearful and neutral postures in the saccadic baseline control task, at 20 ms stimulus duration, from the fearful and neutral saccadic responses at 20-ms cue durations in Experiment 1. Given that no significant differences in SRT between fearful and neutral body postures were observed at 100 ms stimulus durations in the saccadic baseline task or at 100-ms cue durations in Experiment 1, further investigation of the 100 ms data was not warranted.

The difference in SRT of valid fearful trials in Experiment 1 and the baseline fearful saccade (M = 70, SD = 26) was significantly different from the difference in SRT of valid neutral trials and the baseline saccadic latency to neutral postures (M = 48, SD = 30) [t(9) = 2.30, p < 0.05]. Similarly, on invalid trials, the difference in SRT on fearful cue trials and the baseline fearful saccade (M =105, SD = 35) was largely different from the difference in SRT on neutral cue trials and the baseline neutral saccade (M = 64, SD = 38) [t(9) = 5.64, p < 0.001]. Thus, the time to saccade to a single fearful or neutral body posture subtracted from the reaction time on valid and invalid saccadic cue trials in Experiment 1 was used as a control for the attractiveness of each cue. This led to a 22-ms SRT benefit for fearful postures on valid trials and a SRT cost of 41 ms for fearful postures on invalid trials. This cost and benefit enhanced those (13 ms benefit, 7 ms cost) observed in Experiment 1. This suggests that the modulation of attentional cueing observed in Experiment 1 was due to the level of fear expressed in the body postures.

In addition to the saccadic baseline task and breaking the image set down in terms of emotional intensity, another useful and feasible way to disentangle emotional meaning from salient features is to present inverted body stimuli. Like faces (Tanaka & Farah, 1993), body postures have been found to be processed as configurations with body stimuli presented upside down being more difficult to recognize than other inverted stimuli (Reed et al., 2003). In Experiment 2, we presented both upright and inverted fearful body postures. If the cueing effects observed with fearful bodies in Experiment 1 are due to low-level features, then responses towards upright and inverted fearful body cues should be similar since all of the same features are present in both images. If valence is crucial, upright and inverted body cues responses should show divergence.

Experiment 2: Cueing with upright and inverted fearful body postures

Participants

Twenty participants (7 female and 13 male; mean age = 21.8 years; range = 19-34 years) took part. All had normal visual acuity and normal State (M = 31.9, SD = 8) and Trait (M = 32.1, SD = 6) anxiety levels as measured by the State Trait Anxiety Inventory (STAI: Spielberger et al., 1983).

Materials and procedure

The stimuli consisted of body pictures of the same 10 individuals (5 male and 5 female), each displaying a fearful posture, used in Experiment 1. Consistent with Experiment 1, the body pictures subtended on average $6.8^{\circ} \times 17.0^{\circ}$ and were used as cues in the experiment. The target was a $1.5^{\circ} \times 1.5^{\circ}$ fixation cross. Both cue and target stimuli were presented against a uniform white background and were positioned to the left and right of a fixation cross, centered at 9.2° eccentricity, at a viewing distance of 37 cm.

The procedure used was identical to Experiment 1, with the exception that body cues consisted of both upright and inverted fearful postures. No neutral body postures were included in the design. Inverted versions were created by rotating the image through 180°. For each response mode (saccade and manual), each participant performed 320 trials, divided into 8 blocks of 40 trials each (4 blocks at 20-ms cue duration; 4 blocks at 100-ms cue duration). Fifty percent (160) of the experimental trials were valid and 50% (160) were invalid. As with Experiment 1, participants were informed that the body cue would predict the location of the target on some, but not all of the trials.

Results and discussion

Mean RTs are displayed in Figures 3C (saccade mode) and 3D (manual mode). A 2 (mode: saccadic vs. manual response) × 2 (cue duration: 20 ms. vs. 100 ms) × 2 (cue orientation: upright vs. inverted) × 2 (cue validity: valid vs. invalid) ANOVA showed main effects for mode, F(1, 19) = 122.44, MSE = 1280939, p < 0.001, $\eta_p^2 =$.87, cue duration, F(1, 19) = 15.88, MSE = 37671, p < 0.01, $\eta_p^2 = .46$, and cue validity, F(1, 19) = 33.99, MSE = 19438, 9

p < 0.001, $\eta_p^2 = .64$, revealing that participants were faster overall in the saccade (M = 241 ms, SD = 26) compared with manual (M = 368 ms, SD = 40) mode (p < 0.001); at 20-ms (294 ms, SD = 25) compared to 100-ms (M = 315 ms, SD = 23) cue duration (p < 0.01); and when the cue was valid (M = 297 ms, SD = 23) compared with invalid (M =312 ms, SD = 23) (p < 0.001), respectively. There was a significant interaction between Mode \times Cue Duration, $F(1, 19) = 26.59, MSE = 61383, p < 0.001, \eta_p^2 = .58,$ resulting from participants responding faster to the target at 20-ms (M = 217 ms, SD = 23) compared to 100-ms (M =266 ms, SD = 48) cue duration in the saccade mode (p < 1000.001), but showing no significant differences in reaction time between 20-ms (M = 371 ms, SD = 46) and 100-ms (M = 365 ms, SD = 44) cue durations in the manual mode (p = .128). Importantly, the interaction between Cue Orientation \times Cue Validity was also significant, F(1, 19) =8.20, MSE = 2442, p < 0.05, $\eta_p^2 = .30$, demonstrating that the size of the cue validity effect (RT invalid - RT valid) was significantly larger for upright (M = 39 ms, SD = 58) compared to inverted (M = 10 ms, SD = 26) presentation (p < 0.001). No other interactions were significant.

In summary, Experiment 2 showed that upright and inverted body cue responses showed divergence. Notably, inversion of the fearful body cues was found to attenuate the cue validity effect. However, unlike Experiment 1, the cueing effect was not modulated by response mode or cue duration. Despite this, the finding that validity had little effect on inverted fearful faces, while upright fearful faces did show validity effects, suggests that the cueing effects were not simply caused by image artifacts.

Having controlled for low-level image differences, an interesting question still remains. Experiment 1 has shown differences between 20- and 100-ms cue durations, with reaction time being influenced by fearful body cues at 20 ms but not at 100 ms in the saccade mode, with the opposite pattern being observed in the manual mode. However, what is actually happening between 20 and 100 ms which reflects this difference remains to be tested. It is possible that different pathways may be responsible for this difference. To examine this issue, and potentially close in on underlying mechanisms, we conducted a parametric investigation in which cue stimuli were presented for 20-, 40-, 60-, and 100-ms cue durations.

Experiment 3: Parametric investigation

Participants

Twenty participants (14 female and 6 male; mean age = 22.0 years; range = 18-37 years) took part. All had normal visual acuity and normal state (M = 32.7, SD = 5) and

trait (M = 34.3, SD = 4) anxiety levels as measured by the State Trait Anxiety Inventory (STAI; Spielberger et al., 1983).

Materials and procedure

The stimuli and procedure were identical to Experiment 1, except for cue durations which were 20, 40 60, and 100 ms. There were 320 trials (160 saccadic; 160 manual), divided into 8 blocks of 40 trials each (2 blocks at each of the 4 cue durations; 20, 40, 60, and 100 ms). As with the previous experiments, a 50:50 valid/invalid ratio was employed, and participants were informed that the body cue would predict the location of the target on some, but not all of the trials.

Results and discussion

To simplify analysis, mean capture benefits [RT neutral valid - RT fear valid] and disengagement costs [RT fear invalid - RT neutral invalid] were calculated for the fearful postures at each of the four cue durations (20, 40, 60, and 100 ms) in both the saccade and manual response modes.

A 2 (mode) \times 4 (cue duration) ANOVA on the capture scores revealed a significant Mode × Cue Duration interaction, F(3, 57) = 2.94, MSE = 2499, p < 0.05, $\eta_p^2 =$.13. Subsequent paired samples t tests revealed that the capture benefit was significantly larger in the saccade compared to manual mode at 20-ms cue duration [t(19) =2.85, p < 0.05], but no significant differences in the size of the capture benefit emerged between saccadic and manual responses at 40-, 60-, or 100-ms cue durations (all p's > .1). Moreover, as illustrated by Figure 4A, the magnitude of the capture benefit decreased monotonically from 20- to 100-ms cue duration in the saccade mode. The saccadic capture benefit for fearful postures over neutral postures was significant at 20 ms (M = 20 ms, SD = 30) [t(19) =2.93, p < 0.01], marginally significant at 40 ms (M =12 ms, SD 25) [t(19) = 2.03, p = .057], small and nonsignificant at 60 ms (M = 3 ms, SD = 18) [t(19) = 0.67, p =.509], and abolished at 100 ms, where SRTs were faster on valid neutral trials compared to valid fearful trials. In the manual mode, the capture benefit remained consistently small and was non-significant across all four cue durations

A 2 (mode) \times 4 (cue duration) ANOVA on the disengagement scores revealed a significant Mode \times Cue Duration interaction, F(3, 57) = 3.27, MSE = 2376, p <



(all p's > .4).

Figure 4. (A) Mean capture benefit [RT neutral valid – RT fear valid)] and (B) mean disengagement cost [RT fear invalid – RT neutral invalid] for 20-, 40-, 60-, and 100-ms cue durations in the saccade and manual modes. Error bars represent *SEM*.

0.05, $\eta_p^2 = .15$. Subsequent paired samples t tests revealed that the disengagement cost was significantly larger in the manual compared to saccade mode at 100-ms cue duration [t(19) = 2.21, p < 0.05], but no significant differences in the magnitude of the disengagement effect emerged between saccadic and manual responses at 20-, 40-, or 60-ms cue durations (all p's > .2). As illustrated by Figure 4B, there was strong indication that between 20and 100-ms cue durations, the disengagement effect decreased monotonically in the saccade mode. The saccadic disengagement cost for fearful over neutral postures was significant at 20 ms (M = 13 ms, SD = 18) [t(19) = 3.04, p < 0.01], small and non-significant at 40 ms (M = 5 ms, SD = 35) [t(19) = 0.69, p = .501], and abolished at 60 and 100 ms, where SRTs were slower on invalid neutral trials compared to invalid fearful trials. In contrast, the disengagement effect appeared to increase monotonically from 20 to 100 ms in the manual mode. At 20, 40, and 60 ms, the mean manual disengagements costs for fearful over neutral postures were 6 ms (SD = 14), 12 ms (SD = 37), and 14 ms (SD = 39), respectively, although these were non-significant (all p's >.1). At 100 ms, the manual disengagement cost for fearful postures was significant (M = 18, SD = 36) [t(19) = 2.31, p < 0.05].

In summary, Experiment 3 has shown that important differences in the pattern of responses emerge between 20 and 100 ms. There is strong indication that the capture benefit and disengagement cost of fearful body postures monotonically decrease from 20- to 100-ms cue durations in the saccade mode. Furthermore, important differences in the pattern of responses emerged at 40 and 60 ms in the saccade mode. At 40 ms, enhanced attentional capture by fearful body postures was observed, while at 60 ms this effect was abolished. In the manual mode, the disengagement cost of fearful postures was found to increase monotonically from 20 to 100 ms (e.g., 6, 12, 14, 18 ms), while the capture benefit remained consistently small.

General discussion

The present study expanded examinations of threatrelated attentional effects beyond facial expressions and investigated whether threat-related body postures were sufficiently salient to influence the capture and disengagement components of attention in an exogenous cueing task where the duration of the cue (20, 40, 60, and 100 ms) and response mode (saccadic or manual) of interest were systematically varied. The combined findings from the three experiments demonstrate enhanced attentional capture by and also difficulty in disengaging attention from threat-related body postures under specific conditions.

Notably, in the saccade mode, facilitated attentional capture by fearful body postures was observed only at

very rapid cue durations (20 ms: Experiments 1 and 3 and 40 ms: Experiment 3). Likewise, impaired saccadic disengagement from fearful postures was also only observed at the shortest cue duration (20 ms: Experiments 1 and 3). No saccadic emotional modulation (capture or disengagement) was observed at 60-ms (Experiment 3) or 100-ms cue durations (Experiments 1 and 3), suggesting that even very small changes in SOA can impact upon saccade patterns. Conversely, in the manual mode, no emotional modulation (capture or disengagement) was observed at 20-, 40-, or 60-ms cue durations. However, at the longer cue duration (100 ms), the valence of the body cue did modulate attention marginally, but this effect was only evident for the disengagement component, not capture. Taken together, the findings suggest that fear conveyed through body posture has the power both to capture and to subsequently hold attention. As demonstrated from Experiment 2, where cueing responses for upright and inverted fearful body postures showed divergence, this modulation of attention appears to result from the respective valence of the fearful body posture, not from any low-level images differences. Importantly, we have replicated this pattern of results in further studies, using face stimuli (Bannerman, Milders, & Sahraie, in press), which not only attests to the reliability of the findings but also supports previous research suggesting that body and face stimuli are processed in a similar manner (Bannerman, Milders, de Gelder, et al., 2009; Hadjikhani & de Gelder, 2003; Meeren et al., 2005; Reed et al., 2003; van Heijnsbergen et al., 2007).

Besides from showing that fearful body postures can modulate attentional effects, thus showing that fear conveyed through body postures can act as a salient signal of imminent danger in the absence of any face cues, the data also revealed some other intriguing findings. Of particular interest were the different time courses for saccadic and manual threat-related cueing effects. At 20-ms cue duration, the saccadic RT data showed facilitated attentional capture and impaired disengagement from fearful body postures. By contrast, the manual RT data at 20 ms revealed no cueing modulation. This is consistent with a previous study which used a rapid (e.g., 28 ms) cue duration and found no modulation of attention by emotion using manual responses (Koster et al., 2007). This finding was initially taken as evidence that rapid cue durations are too short to allow sufficient time for extracting the threatening value of a stimulus. However, the saccade data reported here and in previous investigations (Bannerman et al., in press) show that brief (20 ms) cue durations are sufficient to extract threat-related information and this threat information is subsequently used to modulate cueing effects. Notably, being able to orient quickly to briefly presented threat is of high relevance for safety and is in line with ERP studies which have shown that early electrophysiological markers react to threat-related information even after very short presentation times (Fox et al., 2008).

Interestingly, it has been argued that the exogenous cueing task is especially sensitive in measuring attentional disengagement effects, while attentional capture effects are less frequently reported (Fox et al., 2001, 2002). The attentional capture component, based on manual RT data, has even been described as an encapsulated process, not modulated by the emotional meaning of the cue (Fox et al., 2001). However, the saccade data reported here show that it is not an encapsulated process, in that facilitated attentional capture with threat-related body postures can be observed in the emotional exogenous cueing paradigm. This fits well with current theories (Le Doux, 1996; Mathews & Mackintosh, 1998; Öhman & Mineka, 2001), which state that we have a predisposition to orientate towards threat, even when it is presented briefly. Nevertheless, the fact that no emotional modulation was observed at 60- and 100-ms cue durations in the saccade mode may suggest that facilitated attentional orienting to and increased attentional hold time on threat-related information, at least when measured with saccades, is a short-lived phenomenon. It would appear that at 60- and 100-ms cue durations in the saccade mode, we can successfully inhibit threat-related information.

In contrast, the manual data at 100-ms cue duration did reveal cueing effects, with fearful body postures leading to marginally delayed disengagement compared to neutral body postures. This finding is consistent with previous studies using longer cue durations (e.g., 100, 250, 500 ms), which have found that threat-related stimuli (including negative facial expressions, aversive words, and aversive scenes) are especially effective in holding visual attention (Bannerman et al., in press; Fox et al., 2001, 2002; Yiend & Mathews, 2001). Interestingly, such findings were initially reported only in highly anxious individuals (but see Koster et al., 2004, 2007). However, our findings show that threat-related information influences the capture and disengagement components of attention with saccades and the disengagement component of attention with manual responses in normal, healthy individuals. These findings are consistent with attentional models of threat which posit that prioritization of threat-related signals is a normal and adaptive mechanism present in all of us (Mathews & Mackintosh, 1998). Moreover, given that fearful body postures were able to modulate attentional effects in the exogenous cueing task in a similar fashion previously observed with fearful faces (Bannerman et al., in press) may point towards the perception of faces and bodies being subserved by similar underlying neural mechanisms. Electrophysiological, neuroimaging, and neuropsychological findings corroborate with this view. Namely, viewing fearful compared with neutral body expressions produces an early emotion effect on the P1 peak latency (112 ms) after the stimulus onset (van Heijnsbergen et al., 2007), comparable to that reported for fearful faces (Righart & de Gelder, 2006); the fusiform cortex and the amygdala are central to the processing of fearful body expressions (Hadjikhani & de Gelder, 2003) as well as for fearful facial expressions (Kanwisher et al., 1997; Morris et al., 1998); and bilateral amygdala damage can lead to an equivalent deficit at recognizing fear from facial expressions and body postures (Sprengelmeyer et al., 1999).

Importantly, the different time course of saccadic and manual cueing effects is at odds with a parsimonious model, which posits that a single, central process affects all reaction time measures in a similar fashion. Instead, performance in the current study may suggest that saccades and manual responses at least in part rely on distinct mechanisms. These mechanisms appear to differ in their processing times, resulting in the disparate findings reported. Supporting the view that saccades and manual responses do not fit within a parsimonious model, a recent study reported reaction time differences between luminance and short wavelength specific stimuli, with RT differences being twice as large for saccadic responses than for manual responses (Bompas & Sumner, 2008). This may imply that saccades are driven more by fast signals than are manual responses. Fast signals are also associated with subcortical processing via the superior colliculus (SC). Importantly, the retinotectal pathway that projects directly from the retina to the SC is known to play a prominent role in the generation of saccades (Bompas & Sumner, 2008). Furthermore, there is also evidence of a subcortical route to the amygdala involved in rapid, survival-enhancing responses towards threatrelated stimuli (Le Doux, 1996). Of importance here are the SC and the pulvinar whose nuclei are activated by viewing fearful faces (Morris, de Gelder, Weiskrantz, & Dolan, 2001) and also fearful body postures (de Gelder et al., 2004). Notably, the subcortical route postulated by Le Doux (1996) functions optimally when stimuli are briefly flashed and capture attention, consistent with the larger saccadic cueing effects observed at brief (20 ms) compared to longer (100 ms) cue durations in the current study.

In summary, the current experiments have shown that the quick capturing of attention by threat conveyed through body posture is dependent upon response mode. Saccades influence both the capture and disengagement components of attention, but only at very rapid (20 ms) cue durations. Manual responses, conversely, do not show cueing effects at rapid cue durations; they instead influence the disengagement component of attention over more extended periods of time.

Acknowledgments

We thank Mr. James Urquhart for technical support, Prof. Beatrice de Gelder for help with stimuli, and Dr. Amelia Hunt for comments on earlier versions of the manuscript. R.L.B. is supported by postgraduate scholarships from the Aberdeen Endowments Trust and Robert Nicol Trust. Commercial relationships: none. Corresponding author: Rachel L. Bannerman. Email: r.bannerman@abdn.ac.uk. Address: School of Psychology, University of Aberdeen,

References

AB24 2UB, UK.

- Bannerman, R. L., Milders, M., de Gelder, B., & Sahraie, A. (2009). Orienting to threat: Faster localization of fearful facial expressions and body postures revealed by saccadic eye movements. *Proceedings of the Royal Society of London B: Biological Science*, 276, 1635–1641. [PubMed]
- Bannerman, R. L., Milders, M., & Sahraie, A. (2009). Processing emotion: Comparison of saccadic and manual choice-reaction times. *Cognition and Emotion*, 23, 930–954.
- Bannerman, R. L., Milders, M., & Sahraie, A. (in press). Attentional bias to brief threat-related faces revealed by saccadic eye movements. *Emotion*.
- Bompas, A., & Sumner, P. (2008). Sensory sluggishness dissociates saccadic, manual, and perceptual responses: An S-cone study. *Journal of Vision*, 8(8):10, 1–13, http://journalofvision.org/content/8/8/10, doi:10.1167/ 8.8.10. [PubMed] [Article]
- Bradley, B. P., Mogg, K., Falla, S., & Hamilton, L. R. (1998). Attentional bias for threatening facial expressions in anxiety: Manipulations of stimulus duration. *Cognition and Emotion*, 12, 737–753.
- Bradley, B. P., Mogg, K., & Millar, N. H. (2000). Covert and overt orientation of attention to emotional faces in anxiety. *Cognition and Emotion*, *14*, 789–808.
- Brandman, T., & Yovel, G. (2010). The body inversion effect is mediated by face-selective not body-selective brain areas. *Journal of Vision*.
- de Gelder, B., Snyder, J., Greve, D., Gerard, G., & Hadjikhani, N. (2004). Fear fosters flight: A mechanism for fear contagion when perceiving emotion expressed by a whole body. *Proceedings of the National Academy of Sciences of the United States* of America, 101, 16701–16706. [PubMed] [Article]
- Fischer, B., & Weber, H. (1993). Express saccades and visual attention. *Behavioral and Brain Sciences*, *16*, 533–610.
- Fox, E., Derakshan, N., & Shoker, L. (2008). Trait anxiety modulates the electrophysiological indices of rapid spatial orienting towards angry faces. *Neuroreport*, 19, 259–263.
- Fox, E., Lester, V., Russo, R., Bowles, R. J., Pichler, A., & Dutton, K. (2000). Facial expressions of emotion: Are angry faces detected more efficiently? *Cognition and Emotion*, 14, 61–92.

- Fox, E., Russo, R., Bowles, R., & Dutton, K. (2001). Do threatening stimuli draw or hold visual attention in subclinical anxiety? *Journal of Experimental Psychology: General*, 130, 681–700. [PubMed] [Article]
- Fox, E., Russo, R., & Dutton, K. (2002). Attentional bias for threat: Evidence for delayed disengagement from emotional faces. *Cognition and Emotion*, *16*, 355–379.
 [PubMed] [Article]
- Hadjikhani, N., & de Gelder, B. (2003). Seeing fearful body expressions activates the fusiform cortex and amygdala. *Current Biology*, 13, 2201–2205. [PubMed]
- Hermans, D., Vansteenwegen, D., & Eelen, P. (1999). Eye movement registration as a continuous index of attention deployment: Data from a group of spider anxious students. *Cognition and Emotion*, *3*, 419–434.
- Hunt, A. R., Cooper, R., Hungr, C., & Kingstone, A. (2007). The effect of emotional faces on eye movements and attention. *Visual Cognition*, *15*, 513–531.
- Hunt, A. R., van Zoest, W., & Kingstone, A. (2010). Attending to emerging representations: The importance of task context and time of response. In A. K. Nobre & J. Coull (Eds.), *Attention and time*. Oxford, England: Oxford University Press.
- Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: A module in human extrastriate cortex specialized for face perception. *Journal of Neuroscience*, *17*, 4302–4311. [PubMed] [Article]
- Kaylesnykas, R. P., & Hallett, P. E. (1987). The differentiation of visually guided and anticipatory saccades in gap and overlap paradigms. *Experimental Brain Research*, 68, 115–121.
- Kissler, J., & Keil, A. (2008). Look don't look! How emotional pictures affect pro- and antisaccades. *Experimental Brain Research*, 188, 215–222.
- Koster, E.-H.-W., Crombez, G., Van Damme, S., Verschuere, B., & De Houwer, J. (2004). Does imminent threat capture and hold attention? *Emotion*, *4*, 312–317. [PubMed]
- Koster, E. H. W., Crombez, G., Verschuere, B., Van Damme, S., & Wiersema, J. R. (2006). Components of attentional bias to threat in high trait anxiety: Facilitated engagement, impaired disengagement, and attentional avoidance. *Behaviour Research and Therapy*, 44, 1757–1771. [PubMed]
- Koster, E. H. W., Crombez, G., Verschuere, B., Vanvolsem, P., & De Houwer, J. (2007). A timecourse analysis of attentional cueing by threatening scenes. *Experimental Psychology*, 54, 161–171. [PubMed]
- Le Doux, J. E. (1996). *The emotional brain*. New York: Simon & Schuster.

- Lundqvist, D., & Öhman, A. (2005). Emotion regulates attention: The relation between facial configurations, facial emotion and visual attention. *Visual Cognition*, *12*, 51–84.
- Mathews, A., & Mackintosh, B. (1998). A cognitive model of selective processing in anxiety. *Cognitive Therapy and Research*, *22*, 539–560.
- Meeren, H. K., van Heijnsbergen, C. C., & de Gelder, B. (2005). Rapid perceptual integration of facial expressions and emotional body language. *Proceedings of the National Academy of Sciences of the United States of America*, 102, 16518–16423. [PubMed] [Article]
- Mogg, K., & Bradley, B. P. (1999). Orienting of attention to threatening facial expressions presented under conditions of restricted awareness. *Cognition and Emotion*, 13, 713–740.
- Morris, J. S., de Gelder, B., Weiskrantz, L., & Dolan, R. J. (2001). Differential extrageniculostriate and amygdala responses to presentation of emotional faces in a cortically blind field. *Brain*, 124, 1241–1252. [PubMed]
- Morris, J. S., Friston, K. J., Büchel, C., Frith, C. D., Young, A. W., Calder, A. J., et al. (1998). A neuromodulatory role for the human amygdala in processing emotional facial expressions. *Brain*, 121, 47–57. [PubMed]
- Nummenmaa, L., Hyöna, J., & Calvo, M. (2006). Eye movement assessment of selective attentional capture by emotional pictures. *Emotion*, 6, 257–268. [PubMed]
- Ohman, A., Lundqvist, D., & Esteves, F. (2001). The face in the crowd revisited: A threat advantage with schematic stimuli. *Journal of Personality and Social Psychology*, 80, 381–396. [PubMed]
- Öhman, A., & Mineka, S. (2001). Fears, phobias, and preparedness: Toward an evolved module of fear and fear learning. *Psychological Review*, 108, 483–522. [PubMed]
- Pessoa, L., McKenna, M., Gutierrez, E., & Ungerleider, L. G. (2002). Neural processing of emotional faces

requires attention. *Proceedings of the National Academy of Sciences of the United States of America*, 99, 11458–11463. [PubMed] [Article]

- Posner, M. I. (1980). Orientation of attention. *Quarterly Journal of Experimental Psychology*, 32, 3–25.
- Reed, C. L., Stone, V. E., Bozova, S., & Tanaka, J. (2003). The body-inversion effect. *Psychological Science*, 14, 302–308. [PubMed]
- Righart, R., & de Gelder, B. (2006). Context influences early perceptual analysis of faces: An electrophysiological study. *Cerebral Cortex*, 16, 1249–1257. [PubMed]
- Saslow, M. G. (1967). Latency for saccadic eye movement. *Journal of the Optical Society of America*, 57, 1030–1033. [PubMed]
- Spielberger, C. D., Gorsuch, R. L., Lushene, R., Vagg, P. R., & Jacobs, G. A. (1983). *State-trait anxiety inventory*. Palo Alto, CA: Consulting Psychologists Press.
- Sprengelmeyer, R., Young, A. W., Schroeder, U., Grossenbacher, P. G., Federlein, J., Büttner, T., et al. (1999) Knowing no fear. *Proceedings of the Royal Society of London B: Biological Science*, 266, 2451–2456. [PubMed] [Article]
- Tanaka, J. W., & Farah, M. J. (1993). Parts and wholes in face recognition. *Quarterly Journal of Experimental Psychology A: Human Experimental Psychology*, 46, 225–245. [PubMed]
- Van den Stock, J., Righart, R., & de Gelder, B. (2007). Body expressions influence recognition of emotions in the face and voice. *Emotion*, 7, 487–494. [PubMed]
- van Heijnsbergen, C. C. R. J., Meeren, H. K. M., Grezes, J., & de Gelder, B. (2007). Rapid detection of fear in body expressions, an ERP study. *Brain Research*, 1186, 233–241. [PubMed]
- Yiend, J., & Mathews, A. (2001). Anxiety and attention to threatening pictures. *Quarterly Journal of Experimental Psychology A: Human Experimental Psychology*, 54, 665–681. [PubMed]
- Yovel, G., & Kanwisher, N. (2005). The neural basis of the face inversion effect. *Current Biology*, 15, 2256–2262. [PubMed]