

Emotion and action: the effect of fear on saccadic performance

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Abstract According to evolutionary accounts, emotions originated to prepare an organism for action (Darwin 1872; Frijda 1986). To investigate this putative relationship between emotion and action, we examined the effect of an emotional stimulus on oculomotor actions controlled by the superior colliculus (SC), which has connections with subcortical structures involved in the perceptual prioritization of emotion, such as the amygdala through the pulvinar. The pulvinar connects the amygdala to cells in the SC responsible for the speed of saccade execution, while not affecting the spatial component of the saccade. We tested the effect of emotion on both temporal and spatial signatures of oculomotor functioning using a gap-distractor paradigm. Changes in spatial programming were examined through saccadic curvature in response to a remote distractor stimulus, while changes in temporal execution were examined using a fixation gap manipulation. We show that following the presentation of a task-irrelevant fearful face, the temporal but not the spatial component of the saccade generation system was affected.

Keywords Saccades · Superior colliculus · Emotion · Action

Introduction

There is now considerable evidence that emotive processing has widespread effects on human perceptual and attentional functioning. For example, visual search tasks have

revealed that searches for emotional stimuli are more efficient than those for neutral stimuli (e.g., Eastwood et al. 2003; Öhman et al. 2001), and manual response times to targets following emotional content are faster compared to those following neutral content (Fox et al. 2002; 2001). In addition, perceptual detection thresholds for emotional content have been found to be lower than non-emotional stimuli (Calvo and Esteves 2005), and the perception of emotional content has been shown to be accelerated in time compared to competing neutral information (West et al. 2009). This prioritized perception of emotional stimuli is thought to occur through a fast-acting subcortical pathway originating from magnocellular retinal inputs which include reciprocal connections between the superior colliculus (SC), pulvinar, and amygdala (Ledoux 2000; Linke et al. 1998; Amaral et al. 1992). Indeed, disrupting the magnocellular pathway suppresses this observed prioritization of emotional content in a scene (West et al. 2010).

While these studies demonstrate a perceptual and/or attentional prioritization of emotionally valenced stimuli that imply the involvement of action-based systems, a direct measure of motor action was not employed; thus, the functional benefit derived from these processes is still not well understood. Why do we preferentially attend to and process emotional content at the expense of competing non-affective information? According to Darwin (1872), emotions are evolutionary adaptations derived from actions, which suggests that emotional stimuli should be processed rapidly and efficiently. This association of emotional content with the functional significance of motor vigilance still exists in more contemporary discussions (e.g., Frijda 1986), yet little empirical evidence for this relationship has been demonstrated. The subcortical pathway responsible for the prioritization of emotional content includes not only structures such as the amygdala, which

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is implicated in the expedient extraction of emotional information within a scene, but also includes the pulvinar and the SC, which are intimately involved in the production of saccadic motor output. Given the contribution of these visuomotor regions to emotion processing, and the existence of few studies directly examining the effect of a passively displayed emotional stimulus on motor output, we reasoned that the oculomotor system could serve as a useful platform for studying the relationship between emotions and action.

To examine the effect of emotional stimuli on saccadic motor output, we used task irrelevant displays of fearful faces in conjunction with a gap-distractor paradigm. Participants were directed to make saccades to a target “X” in the presence of a distractor “O”, while centrally fixating on either a fearful or neutral facial display. We used fear displays due to their demonstrated ability to bias both attentional and perceptual resources (e.g., West et al. 2009; Phelps et al. 2006; Anderson and Phelps 2001), and the gap-distractor paradigm because it allowed us to concurrently measure two distinct oculomotor processes that are controlled by the SC: one temporal and one spatial.

The temporal component of saccades was measured through the presence or absence of the fixation object, the well-known gap effect. This effect, first reported by Saslow (1967) and replicated numerous times (see Jin and Reeves 2009 for a recent review), is a dramatic reduction in saccadic latencies when a fixated object disappears just prior to the appearance of a target object. In the present experiment, this was accomplished by having the centrally displayed face either be removed before the onset of a peripheral saccade target (gap trials) or remain onscreen throughout the duration of the trial (overlap trials). Neurophysiologically, the gap effect occurs because the removal of the fixated object decreases the tonic activity of fixation neurons, and increases the activity of build-up neurons, in the intermediate layers of the SC (Munoz and Fecteau 2002). Importantly, the pulvinar (part of the subcortical emotion circuit) has connections with the caudate nucleus (Leh et al. 2008). The caudate has an inhibitory connection with the substantia nigra, which in turn has an inhibitory connection to the intermediate layer of the SC (Hikosaka and Sakamoto 1986). Thus, activity in the caudate reduces activity in the substantia nigra, which in turn reduces tonic inhibition in the SC. The prediction stemming from the connections between the pulvinar and the SC is that when the fixation object is removed, saccadic latencies should be reduced in fear face trials compared to neutral face trials (i.e., a larger gap effect for fear face trials).

The spatial component of the saccade was measured through saccadic trajectory curvature toward or away from the target in the presence of the distractor. Several studies have shown that when a distractor is present in the periph-

ery, short latency saccades tend to curve toward the distractor, while long latency saccades tend to curve away from the distractor (e.g., McSorley et al. 2006; Van der Stigchel and Theeuwes 2005; Campbell et al. 2009). These deviations are due to the interplay of fast excitatory stimulus-driven signals and slow inhibitory top-down signals that are integrated within the SC. Initially, the distractor and target activity on the SC are averaged into a single vector, and the eye curves toward the distractor. As time goes by, cortical inhibition projected from the frontal eye fields (FEFs) onto the SC causes the distractor location to be inhibited below baseline levels and the eye curves away from the distractor (McSorley et al. 2006; Walker et al. 2006). Importantly, this inhibition is thought to be specific to the site of the distractor on the neural oculomotor map of the SC and should be unrelated to the tonic inhibition supplied to the SC from the substantia nigra. Because of this, emotion-based changes in the activity of the pulvinar should not affect deviations in saccadic trajectories due to peripheral distractors. In addition, previous imaging work has demonstrated the existence of distinct neural mechanisms involving the FEF and a pulvinar/substantia nigra network that independently supply inhibition to the SC (Gitelman et al. 2002; Nobre et al. 1997). When considering these factors, we expect to find differences in the temporal component stemming from substantia nigra inhibition (gap effect), but not the spatial inhibitory component from the FEFs (trajectory deviations), of saccades between fear and neutral face trials.

Method

Participants

Participants were 20 undergraduates (18–23; $M = 19.13$, $SD = 3.30$) at the University of Toronto who received partial course credit for their participation. All participants reported having normal or corrected to normal vision.

Apparatus and stimuli

Eye movements were recorded by monitoring pupil position and corneal reflectance using a camera-based eye tracker (SR Research Eyelink 1,000) with a temporal resolution of 1,000 Hz and an RMS spatial resolution of 0.01° of visual angle. Gaze position was established using a nine-point calibration and validation scheme. The beginning and the end of saccadic eye movements were determined using a $30^\circ/s$ threshold with the additional criteria that the eye exceeded an acceleration of $8,000^\circ/s$ during the movement. Experimental displays were presented on a 19 in. flat CRT at a refresh rate of 85 Hz and a resolution of $1,024 \times 768$

pixels. A chin rest was used to fix participants' heads 80 cm from the monitor.

Stimuli were 17 fear and 17 neutral faces taken from two standard data sets of cross-culturally recognized posed facial expressions (Ekman and Friesen 1976; Matsumoto and Ekman 1988). To minimize variation in facial feature positions, each stimulus was rigidly aligned such that the centers of the eyes and the tip of the nose were equated across images. Facial contours were equated by cropping each face using a consistent oval that retained the eyebrows, eyes, nose, and mouth in each image. Finally, lighting differences were globally equated using histogram equalization. All of these image-processing steps were carried out in Matlab 7.0.

Procedure

Each experimental session began with eye-tracker setup during which calibration and validation were performed repeatedly until a minimum average accuracy of 0.5° was attained. Participants then completed one block of 8 practice trials, followed by eight blocks of 41 experimental trials distributed evenly across all experimental conditions.

Between blocks, the experimenter could elect to recalibrate the eye tracker. Every trial began with a fixation stimulus (a white ring with an outer diameter of 0.35° and an inner diameter of 0.16°) that was presented in the center of the display on a light-grey background (see Fig. 1 for a typical trial sequence). Once participants moved their gaze to within 1.5° of the fixation stimulus (all reported distances are from the center of a stimulus), they were required to maintain fixation within this region for a randomly determined duration between 800 and 1,300 ms, at which point a fearful or neutral face was equally likely to be presented centered at fixation and subtending 8.10° by 9.10° . The face stimulus either remained on screen for 200 ms followed by a 200 ms gap before the target stimuli appeared on screen, or the face stimulus remained on screen throughout the duration of the trial, thus creating gap and overlap conditions. On all trials, a warning tone (1,000 Hz; 100 ms) was presented 200 ms before the onset of the target stimuli.

Both the target and distractor stimuli appeared simultaneously. The target was a white cross and always appeared 8.0° above, below, to the left of, or to the right of the fixation stimulus. The distractor was a white circle that could appear in the four locations that were 8.0° from the fixation

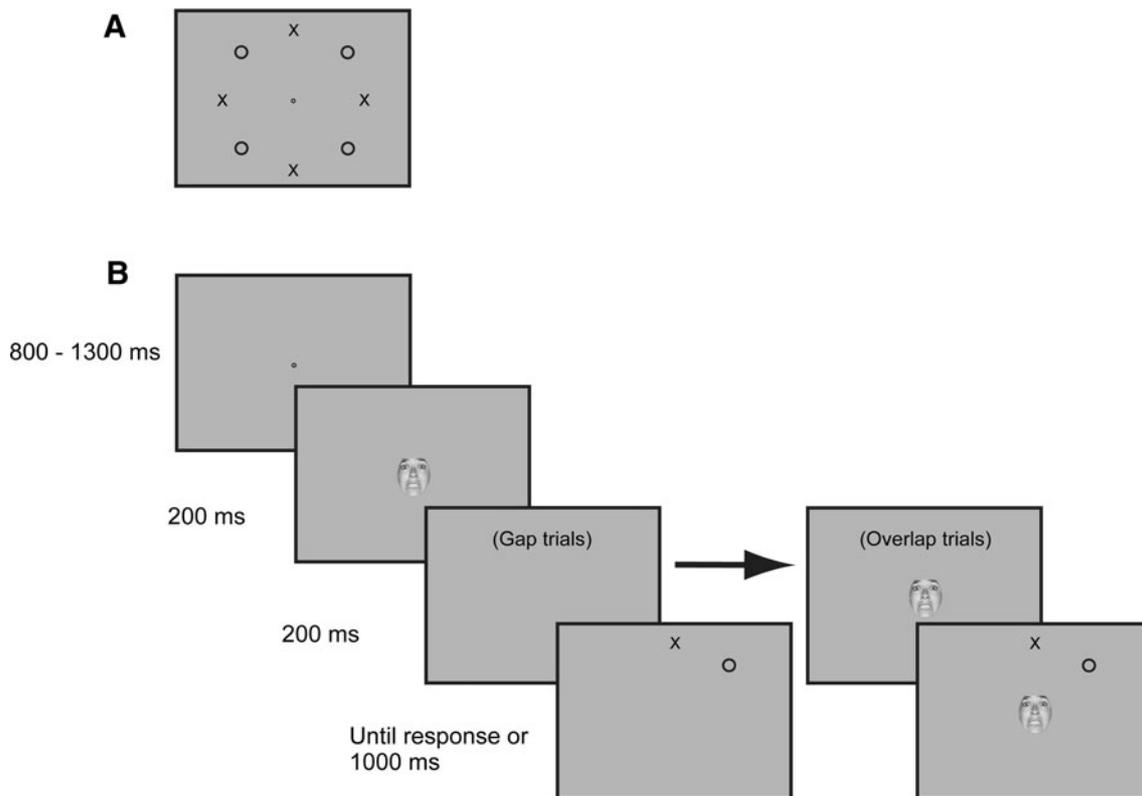


Fig. 1 **a** Depiction of the potential target (X's) and distractor (O's) locations. **b** A typical trial sequence. Participants fixated on the central circle that was replaced by either a fearful or neutral face. On gap trials, the face offset for 200 ms before the target and distractor appeared. On

overlap trials, the face remained onscreen for the duration of the trial. Participants were required to make a saccade toward the target upon its presentation. The target always appeared concomitantly with a distractor in one of the two target-adjacent locations

stimulus and equidistant from adjacent target locations. The distractor was always presented in one of the two locations directly adjacent to the target. Both the target and the distractor subtended 1.0° horizontally and vertically, and were drawn with line widths of 0.1° . Once the target was present, participants were required to move their gaze to within 3° of the target stimulus using a single saccade. If participants failed to maintain fixation before the target was presented, a 200-Hz error tone sounded for 100 ms, the display items were extinguished for 750 ms, and then the trial recommenced. If fixation failed three times consecutively, the experimenter could choose to recalibrate the eye tracker. After the target was presented, if participants failed to initiate a saccade within 1,000 ms, or failed to move their eyes to the target location first, the error tone sounded and an error was recorded. At the end of a trial, the display items remained on the display for 250 ms and were then removed for an inter-trial interval of 600 ms. The trials from the four different target locations were collapsed for analysis, creating a 2 (Gap: gap vs. overlap) \times 2 (Emotional Display: fearful face vs. neutral face) design that was fully crossed within subjects.

Measures

There were two dependent measures used to evaluate the effect of emotional displays on changes in the time course of saccadic trajectory deviations: saccadic reaction time (SRT) and saccadic curvature. SRT was calculated as the latency between the onset of the target stimulus and the onset of the target directed saccade. Saccadic curvature was calculated using the quadratic method put forth by Ludwig and Gilchrist (2002). Namely, the trajectory of each saccade was scaled and translated to travel a common absolute distance, and the best-fitting quadratic polynomial to the trajectory was determined. The coefficient of the quadratic term of the resulting polynomial provides the measure of the amplitude of curvature, which is reported in hundredths of a degree of visual angle. To reveal the time course of curvature, each participant's SRTs were vintalized into five bins (Vincent 1912). Each bin contained one quintile of a participant's SRTs, and the mean curvature for the responses in each bin was calculated. Changes in mean curvature across bins were used to infer changes in saccadic curvature over time (McSorley et al. 2006).

Results

Error trials ($M = 12.45\%$, $SD = 6.20$) were excluded from the reported analyses. As well, trials were trimmed from each participant's data set using a three standard deviation threshold, first based on SRT and then curvature (2.32%).

We first examined whether the emotional displays affected saccadic curvature. As in previous examinations of the saccade trajectory time-course, we collapsed across the Gap condition. The inclusion of both gap and overlap trials creates additional variability that allows the trajectory time course to be observed across an extended range of SRTs (Campbell et al. 2009; McSorley et al. 2006). The time course of saccadic trajectories broken down by emotional condition is shown in Fig. 2a. As predicted, there are virtually no differences in saccadic curvature between trials where displays of fearful and neutral faces were presented. This was evident for both saccades of shorter and longer latencies. To confirm this lack of difference, a linear regression of curvature onto SRT was performed for each participant using the vintalized means, and the mean slope and intercept of these lines were compared between both conditions. As can be seen in Fig. 2a, the mean slope (in hundredths of a degree per ms) was not significantly steeper on fear trials ($M = -0.09$, $SD = 0.06$) than neutral trials

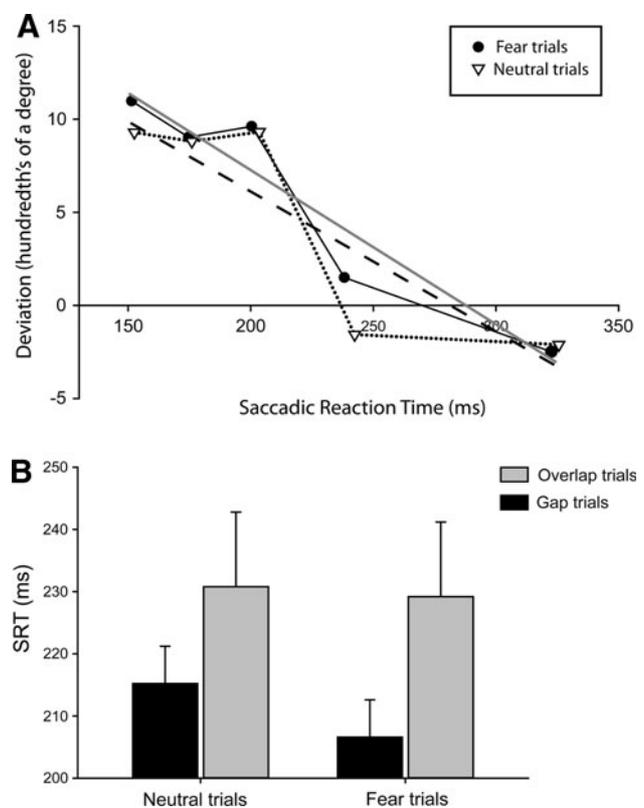


Fig. 2 **a** Trajectory deviations vintalized by saccadic reaction time shown as a function of emotional condition. Each participant's trials were divided into five bins based on reaction time (RT), one for each quintile of participant's SRT distribution. The mean SRT (*x*-axis) and mean curvature (*y*-axis) for one bin is reflected in each point. The linear regression line of curvature onto SRT is also plotted for both fear trials (*solid line*) and neutral trials (*dashed line*). **b** Saccadic reaction times by gap and emotion conditions. *Error bars* represent one SEM for each condition

($M = -0.10$, $SD = 0.11$), $t < 1$. In addition to this, there was no effect of emotional display on the intercept (fear: $M = 24.99$, $SD = 17.13$; neutral: $M = 24.35$, $SD = 30.06$), $t < 1$.

We next examined the temporal component of saccade functioning by submitting the SRT data to a 2 (Gap: gap vs. overlap) \times 2 (Emotional display: fearful face vs. neutral face) repeated measures ANOVA. This revealed a main effect of gap condition, $F(1,19) = 15.72$, $P < 0.001$, with shorter overall SRTs on gap trials. Of main interest, a significant Gap \times Emotional display interaction was found, $F(1,19) = 5.79$, $P < 0.05$ (see Fig. 2b). Due to the a priori nature of our hypothesis, one tailed t -tests (bonferroni corrected with a threshold of $P < 0.05$) were used to compare saccades initiated after fearful and neutral displays within each gap condition. These tests confirmed that, as predicted, saccades on gap trials were initiated more quickly following displays of fear (206 ms) compared to neutral displays (215 ms; $t(19) = 2.46$, $P < 0.05$). The difference within the overlap condition between saccades initiated following fearful and neutral displays was not significant ($t < 1$).

Discussion

The present study investigated whether a task-irrelevant emotional display could influence oculomotor action through concurrently measuring both a spatial and temporal component of SC functioning. Either fearful or neutral facial displays were presented 200 ms before the appearance of a target and distractor (gap trials), or the facial displays remained on screen throughout the trial (overlap trials). It was predicted that, due to reciprocal connections between structures that form the subcortical emotional circuit (amygdala and pulvinar) and structures involved in the execution of saccades (caudate, substantia nigra, and the SC), emotional displays would affect the temporal aspect of saccadic motor output. Consistent with this hypothesis, a significant interaction between the factor of emotional display and gap condition was found, where gap trials with displays of fear produced faster SRTs compared to those with neutral displays. Conversely, it was thought that emotional displays would not affect the spatial programming of saccades due to the lack of direct connections between slower acting cortical inhibition from the frontal eye fields onto the SC. This was also found to be the case, as analyses of saccadic curvature revealed no significant difference between emotion conditions. Despite the lack of effect of emotion on this measure of saccadic functioning, the distractors did have an overall effect on the spatial programming of saccades, producing the typical time course of saccadic curvature (as seen in Fig. 2a), which indicates that

our measure was sensitive enough to detect changes in saccadic spatial programming (Campbell et al. 2009; McSorley et al. 2006; Van der Stigchel and Theeuwes 2005).

Together, our results suggest that emotional displays do have the ability to affect the temporal but not the spatial aspects of oculomotor action. In other words, the speed in which a saccade is executed is influenced by the passive presence of an emotionally charged stimulus. How does the perception of an emotional stimulus modulate saccadic functioning? Previous reports have demonstrated that emotional stimuli can enhance activity in extrastriate cortex (e.g., Morris et al. 1998), most likely via feed-forward projections directly from the amygdala to retinotopically aligned regions in visual cortex (Rudrauf et al. 2008). This feedback loop is thought to be the neural mechanism responsible for behavioral observations of perceptual bias toward emotional stimuli (West et al. 2009; Fox et al. 2001). This subcortical network includes the pulvinar, which has projections linking the amygdala as well as structures that affect saccade functioning (caudate, substantia nigra, and SC; Leh et al. 2008; Linke et al. 1998; Amaral et al. 1992). As the amygdala acts to rapidly extract emotional information present in the visual array (Anderson et al. 2003; Rudrauf et al. 2008; Whalen et al. 1998), projections from this structure that lead to SC modulation can act to directly affect subsequent oculomotor action.

Few studies to date have examined the effect of emotion on oculomotor action. One such study was conducted by Bannerman et al. (2009), who demonstrated that saccades initiated toward brief presentations of fearful faces or fearful body postures were faster compared to those that were neutral. Similarly, Kissier and Keil (2008) observed faster saccades toward both positive and negative pictures, while Hunt et al. (2007) found evidence for greater degrees of oculomotor capture for schematic emotional faces when they were the target of visual search. Our current results compliment and extend these findings, as we demonstrate that oculomotor vigilance is increased by the mere passive encoding of an emotional display. In addition, our current findings have wider significance to other areas of neuroscience, as the existence of a fast link between the perception of an emotional stimulus and subsequent oculomotor output has implications for the involvement of other motor systems that control limb movements. Further, the existence of a link between emotion and action could have significance for motor rehabilitation programs, as training the nervous system through multiple pathways (Sveistrup 2004) by priming motor responses through emotional content could lead to greater treatment efficacy.

Together, our results demonstrate behaviorally that the subcortical system relying on amygdala-pulvinar-SC connections, long implicated in the perceptual prioritization of

emotional content, provides a link between emotion and action. Further research is needed to investigate the involvement of emotion on other motor processes and to further elucidate the neural substantiation of these behavioral observations.

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