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Red Diffuse Light Suppresses the Accelerated Perception of Fear

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Abstract

Prioritization of affective events may occur via two parallel pathways originating from the retina—a parvocellular (P) pathway projecting to ventral-stream structures responsible for object recognition or a faster and phylogenetically older magnocellular (M) pathway projecting to dorsal-stream structures responsible for localization and action. It has previously been demonstrated that retinal exposure to red diffuse light suppresses M-cell neural activity. We tested whether the fast propagation along the dorsal-action pathway drives an accelerated conduction of fear-based content. Using a visual prior-entry procedure, we assessed accelerated stimulus perception while either suppressing the M pathway with red diffuse light or leaving it unaffected with green diffuse light. We show that the encoding of fearful faces is accelerated, but not when M-channel activity is suppressed, revealing a dissociation that implicates a privileged neural link between emotion and action that begins at the retina.

Keywords

magnocellular, emotion, evolution, action

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The expedient detection of threat in the environment is critical for survival. Conscious experience is, however, selective: A stimulus will either be detected or go unnoticed on the basis of the result of a competition for neural representation between multiple sensory inputs (Beck & Kastner, 2005; Desimone & Duncan, 1995). This raises the question as to how some emotionally salient percepts gain awareness over competing visual information.

One proposal is that a dedicated neural pathway relying on low-spatial-frequency (LSF) information may be responsible for accelerating the extraction of fear-based information from the visual environment (e.g., Rudrauf et al., 2008). How such coarse perceptual representations are able to bias the competition for awareness in favor of fear-based content is, however, not well understood. In the experiments reported here, we examined the hypothesis that the LSF-tuned magnocellular (M) retinal pathway plays a central role during the perceptual acceleration of fear content over other concurrent visual information. The fast-propagating M pathway comprises retinal rod inputs that are maximally tuned for LSF information (Livingstone & Hubel, 1987; Petersen, Miezin, & Allman, 1988; Wiesel & Hubel, 1966) and project to the “where”- and action-oriented dorsal visual stream through cortical and subcortical structures including the superior colliculus, pulvinar, amygdala, and parietal cortex (Linke, De Lima, Schwegler, & Pape, 1999; McDonald, 1998; Schiller, Malpeli, & Schein, 1979).

Conversely, the slower-acting and phylogenetically newer parvocellular (P) retinal pathway, the “what” pathway, is maximally tuned for high-spatial-frequency (HSF) information, providing fine resolution needed for object recognition at the expense of speed (Berson, 1988; Livingstone & Hubel, 1987). Given the dedicated fast propagation of M-pathway projections to dorsal structures responsible for action modulation (Goodale & Westwood, 2004), engagement of this pathway should result in a competitive bias determining the prioritization of objects competing for attention and action.

The dominant origin of M neurons in rod retinal photoreceptors is consistent with the finding that the activity of M neurons is suppressed through exposure to red diffuse light. There is substantive behavioral evidence for this effect (e.g., Breitmeyer & Breier, 1994; Breitmeyer & Williams, 1990; Livingstone & Hubel, 1988). In addition, single-cell recordings in nonhuman primates (e.g., de Monasterio, 1978) and human neuroimaging work (e.g., Bedwell, Brown, McDowell, Yanasak, & Miller, 2006) have demonstrated that red diffuse light attenuates afferents of retinal M channels. We used this manipulation to suppress M-channel activity while testing for

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the accelerated neural selection of fear-based content. A visual prior-entry procedure enabled us to directly assess the temporal prioritization one stimulus received over another, while we either attenuated the M pathway with red diffuse light or left it unaffected with green diffuse light. Prior entry occurs when one stimulus receives increased neural representation over another, and as a result is accelerated in perception (Gibbon & Rutschmann, 1969; Shore, Spence, & Klein, 2001; Stelmach & Herdman, 1991; Ulrich, 1987); in other words, a stimulus that “wins” this race for neural representation will be perceived earlier in time than contemporaneously displayed stimuli. Using this psychophysical technique in conjunction with suppression of M-cell activity through red diffuse light, we found that the accelerated perception of facial fear is dependent on the dorsal-action pathway originating from M-pathway retinal inputs.

Experiment I

We first examined the involvement of the M pathway during the accelerated perception of LSF information. Given the relationship between LSF information and the M pathway, it was important to first establish the general involvement of M retinal inputs during the initial stage of coarse-stimulus prioritization. As LSF-tuned M channels propagate information at a greater speed than HSF-tuned P channels (de Monasterio, 1978), we predicted that an LSF stimulus would be accelerated relative to and thus perceived prior to a concurrently presented competing HSF stimulus. We contrasted LSF and HSF Gabor patches that were enveloped by a Gaussian filter and tilted 180°. These stimuli competed for perceptual representation under conditions of both green and red diffuse light. By assessing the proportion of trials on which a given stimulus was perceived as having first onset as a function of the temporal distribution of the contrasting stimuli, we obtained psychometric functions describing the degree of temporal prioritization—or prior entry—one stimulus received over its contemporary.

Method

Subjects. Seventeen undergraduates from the University of Toronto participated for course credit. All participants were naive to the purpose of the study and had normal or corrected-to-normal vision.

Stimuli and design. Stimuli were presented on a 19-in. ViewSonic (Walnut, CA) Graphic Series G90fb monitor (1024 × 768 resolution; 120-Hz refresh rate). Viewing distance was held constant at 44 cm by a chin rest. A fixation point presented in the center of the screen consisted of a black square (0.1° × 0.1°). The background was either green (RGB values: 0, 125, 0) or red (RGB values: 247, 0, 0), and the displays with red and green diffuse light were equiluminant (14.0 cd/m²). The stimuli were LSF and HSF Gabor patches (sinusoidal

gratings enveloped by a Gaussian filter; 3.0° × 3.0°) with frequencies of 2 cpd and 8 cpd, respectively. They were presented to the left and right of fixation parafoveally, at an eccentricity of 3.0°. To decrease the effect of stimulus anticipation in a particular spatial region, we presented stimulus pairs in either the upper or the lower hemifield at an eccentricity of 2.0°. Stimulus pairs were equally likely to be presented in the upper or the lower hemifield. The stimulus with the first onset was equally likely to be to the left or to the right of fixation. In addition, the two stimuli on a trial had equal chances of having first onset.

Procedure. Each subject participated in a block of 20 practice trials and then 10 experimental blocks of 80 trials (see Fig. 1). The session lasted approximately 1 hr. Subjects viewed the displays binocularly. They were instructed to fixate on the center square, which was presented on screen for a randomly jittered amount of time ranging from 900 to 1,200 ms. Next, the two stimuli were presented, with their onsets separated by a stimulus onset asynchrony (SOA) of 12, 24, 36, 48, or 60 ms. The stimuli remained together on screen for 72 ms and were then occluded during the response phase. The SOA was randomly selected from trial to trial. Subjects were asked to report the temporal order of the stimuli by using their right hand to press the “1” key on the number pad of a keyboard if the left stimulus appeared first and the “3” key if the right stimulus appeared first. Participants were never asked to report the identity of a stimulus, but simply indicated the spatial location of the stimulus that appeared first. Experimental blocks alternated between having the green or the red diffuse light as the display background. The initial lighting condition was randomly selected.

Results

The results for this experiment are summarized in Figure 2. The data were fit to separate sigmoid functions for the two lighting conditions. When Gabor pairs were presented under green diffuse light, prior entry was observed for LSF stimuli, as subjects on average perceived the LSF Gabor stimulus as arriving 13.75 ms prior to a concurrently displayed HSF Gabor stimulus, $t(16) = 3.04, p < .01$. When M-pathway activity was suppressed under red diffuse light, LSF prioritization was highly attenuated, reduced to 1.67 ms, $t(16) = 2.43, p < .05$, a temporal value not significantly differing from zero ($t < 1$). These data indicate that the M pathway is involved in mediating an early acceleration of coarse perceptual information.

Experiments 2a and 2b

Having confirmed that lower-level stimulus prioritization is mediated by coarse LSF stimulus information via the M pathway, we tested whether there is a similar prioritization of higher-level content present in emotional stimuli, such as fear displays. We hypothesized that if fear displays are

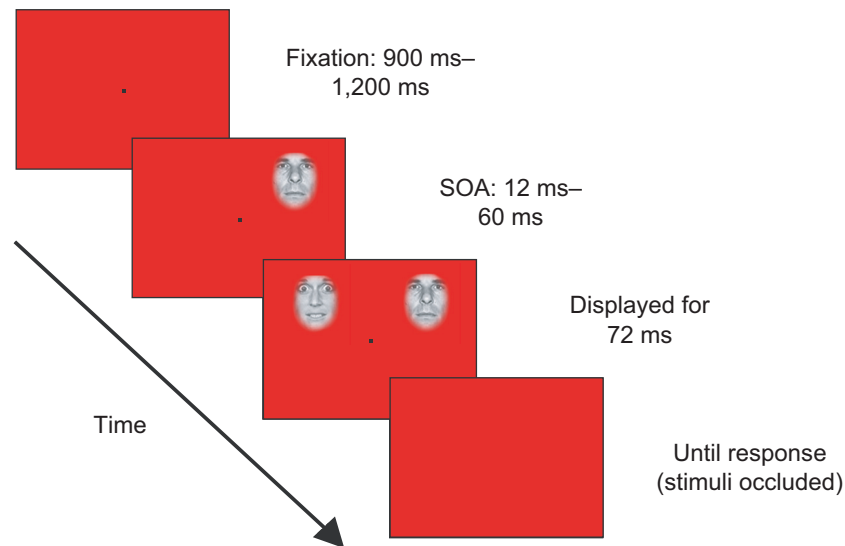


Fig. 1. Illustration of the trial sequence in all four experiments. Prior entry was assessed using a two-alternative forced-choice procedure in which subjects had to report whether the left-hand or the right-hand stimulus appeared first. The two stimuli were separated by a variable stimulus onset asynchrony (SOA). The stimuli were high-spatial-frequency and low-spatial-frequency Gabor patches in Experiment 1, intact and scrambled faces with fearful expressions in Experiment 2a, and faces with neutral and fearful expressions (as shown here) in Experiment 2b. In Experiment 3, the stimuli were horizontal and vertical lines, the range of SOAs used was longer than shown here, and the stimuli remained on screen during the response phase; the task was to indicate whether the vertical or the horizontal line appeared first.

preferentially processed through the M pathway, then their perception should be accelerated, resulting in prior entry. Further, this prior entry for fear displays should occur only

under green diffuse light, and should be suppressed when the M channels are attenuated with red diffuse light. In Experiment 2a, we presented subjects with facial displays of fear

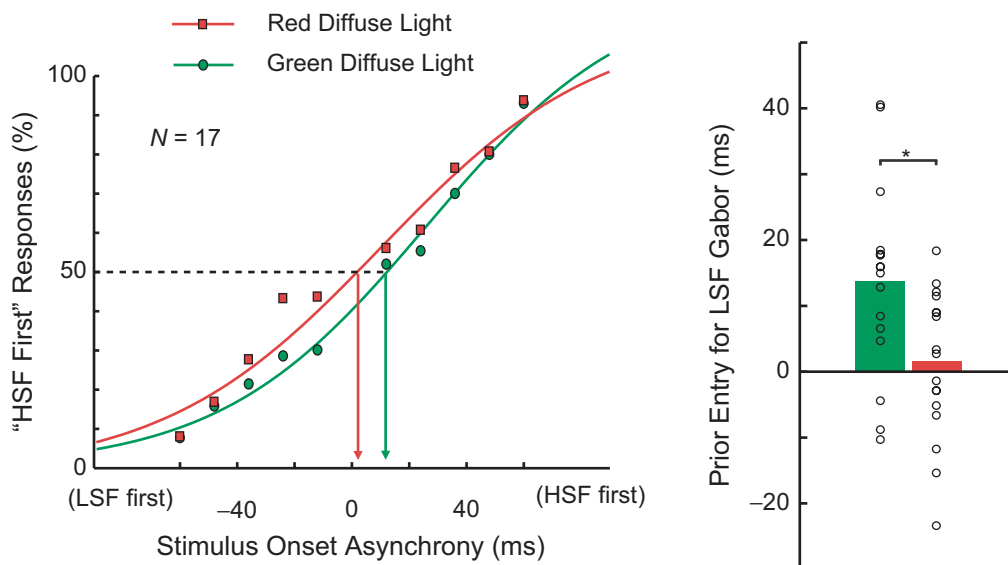


Fig. 2. Results from Experiment 1. The graph on the left presents prior-entry psychometric functions for contrasted Gabor patches. The percentage of responses in which subjects reported the high-spatial-frequency (HSF) stimulus as arriving first is shown as a function of stimulus onset asynchrony (SOA) for conditions of green and red diffuse light. Participants' data were fit to a separate sigmoid function for each lighting condition. Negative SOAs indicate that the low-spatial-frequency (LSF) stimulus was physically presented first, and positive SOAs indicate that the HSF stimulus was physically presented first. The horizontal line intersecting both curves indicates the point where participants perceived the two stimuli as arriving simultaneously (50%). The arrows represent the temporal value of prior entry; positive value indicates prior entry for the LSF stimulus, and a negative value indicates prior entry for the HSF stimulus. The bar graph presents the average temporal value of perceptual acceleration for the LSF stimulus under the two lighting conditions; individual observers' values are overlaid. The bracket refers to the statistical comparison between conditions ($*p < .05$).

that were contrasted with their Fourier scrambled derivatives, in which the global spatial frequencies were maintained and phase was scrambled. Thus, globally, luminance, contrast, and spatial frequencies were held constant between competing stimuli. Psychometric functions were again measured under conditions of red and green diffuse light. In Experiment 2b, we directly contrasted fearful and neutral facial displays to establish whether observed effects of perceptual acceleration could be attributed to the prioritization of fear-based content or simply the prioritization of high-level face content more generally.

Method

Subjects. Two separate groups of 15 undergraduates from the University of Toronto participated in Experiments 2a and 2b for course credit. All participants were naive to the purpose of the study and had normal or corrected-to-normal vision.

Stimuli and design. The stimuli, design, and procedure were almost identical to those of Experiment 1 with the exception that fearful and Fourier-scrambled fearful faces (Experiment 2a) and fearful and neutral faces (Experiment 2b) were used as stimuli competing for awareness. The fearful and neutral face displays were gray-scale photographs of 20 individuals (11 females and 9 males) taken from two standard data sets of cross-culturally recognized posed facial expressions (Ekman & Friesen, 1976; Matsumoto & Ekman, 1988). The faces subtended $4^\circ \times 5^\circ$ of visual angle. Each face stimulus was processed in MATLAB (The MathWorks, Natick, MA) to minimize variation in the positions of facial features; the images were 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. Lighting differences were globally equated using histogram equalization. The Fourier-scrambled stimuli were derived from the processed facial displays of fear; they contained the same spatial frequencies, luminance, and contrast as their original counterparts, but no structure or meaning. Scrambling was accomplished using a two-dimensional fast Fourier transform, followed by phase randomization and reconstruction using the image's original frequency spectrum. A feathering procedure (a softening of the image's edge) was used on the Fourier-scrambled derivatives to minimize the effect of abrupt contrast shifts at the edges of the stimuli. No significant differences in global luminance or contrast levels existed between neutral and fearful faces, or between fearful faces and their Fourier-scrambled counterparts ($t_s < 1$).

Results

The results for Experiments 2a and 2b are summarized in Figures 3a and 3b, respectively. The data were again fit to separate sigmoid functions for the two lighting conditions. We found

that when fear displays and their spatial-frequency-matched derivatives competed under green diffuse light, on average subjects perceived the fear displays as arriving 12.41 ms prior to the scrambled displays, $t(14) = 3.31$, $p < .01$. This perceptual prioritization revealed that fear processing was accelerated in a fashion similar to what we observed for LSF stimuli in Experiment 1. By contrast, M-pathway attenuation under red diffuse light suppressed this fear prioritization, as its temporal value was reduced to an average of 1.90 ms, $t(14) = 3.16$, $p < .01$, which was not significantly different from zero ($t < 1$). These findings indicate that the LSF-tuned M pathway mediates the initial coarse prioritization of facial fear. As global spatial frequencies were constant, these data also provide evidence that the neural mechanism involved is sensitive to higher-level content propagated by the M pathway and not simply to the overall LSF information.

When fearful and neutral facial displays directly competed for perceptual prioritization, we found that fear displays once again were prioritized under green diffuse light, with subjects perceiving fear displays as arriving on average 10.44 ms before competing neutral displays, $t(14) = 2.95$, $p < .01$. This perceptual acceleration of fear was again attenuated when the M pathway was suppressed with red diffuse light, as temporal prioritization was reduced to an average of 1.87 ms, $t(14) = 2.25$, $p < .05$, which did not differ significantly from zero ($t < 1$).

Experiment 3

It is possible that red diffuse light diminishes all sources of competition, thereby reducing temporal-prioritization effects. However, we hypothesized that suppression of the prioritization of fearful faces under red lighting conditions reflects a selective influence on M-pathway stimulus-driven processing. To test this hypothesis, we performed an additional control experiment in which we examined the effect of red light on top-down biasing of ventral-stream competition produced by a predictive arrow cue. We again used the prior-entry paradigm in conjunction with the lighting manipulation, asking participants to judge which of two line stimuli (horizontal or vertical) arrived first. Responses were analyzed as a function of the relative onsets of an uncued stimulus and a stimulus cued by a predictive arrow cue that biased top-down attention to a particular spatial region (see Shore et al., 2001).

Method

Subjects. Ten undergraduates from the University of Toronto participated for course credit. All participants were naive to the purpose of the study and had normal or corrected-to-normal vision.

Procedure. The procedure was similar to that of the previous experiments except that the stimuli were line segments, which were presented in two placeholder boxes to the left and right of fixation on 50% of the trials. On these bilateral trials, a centrally

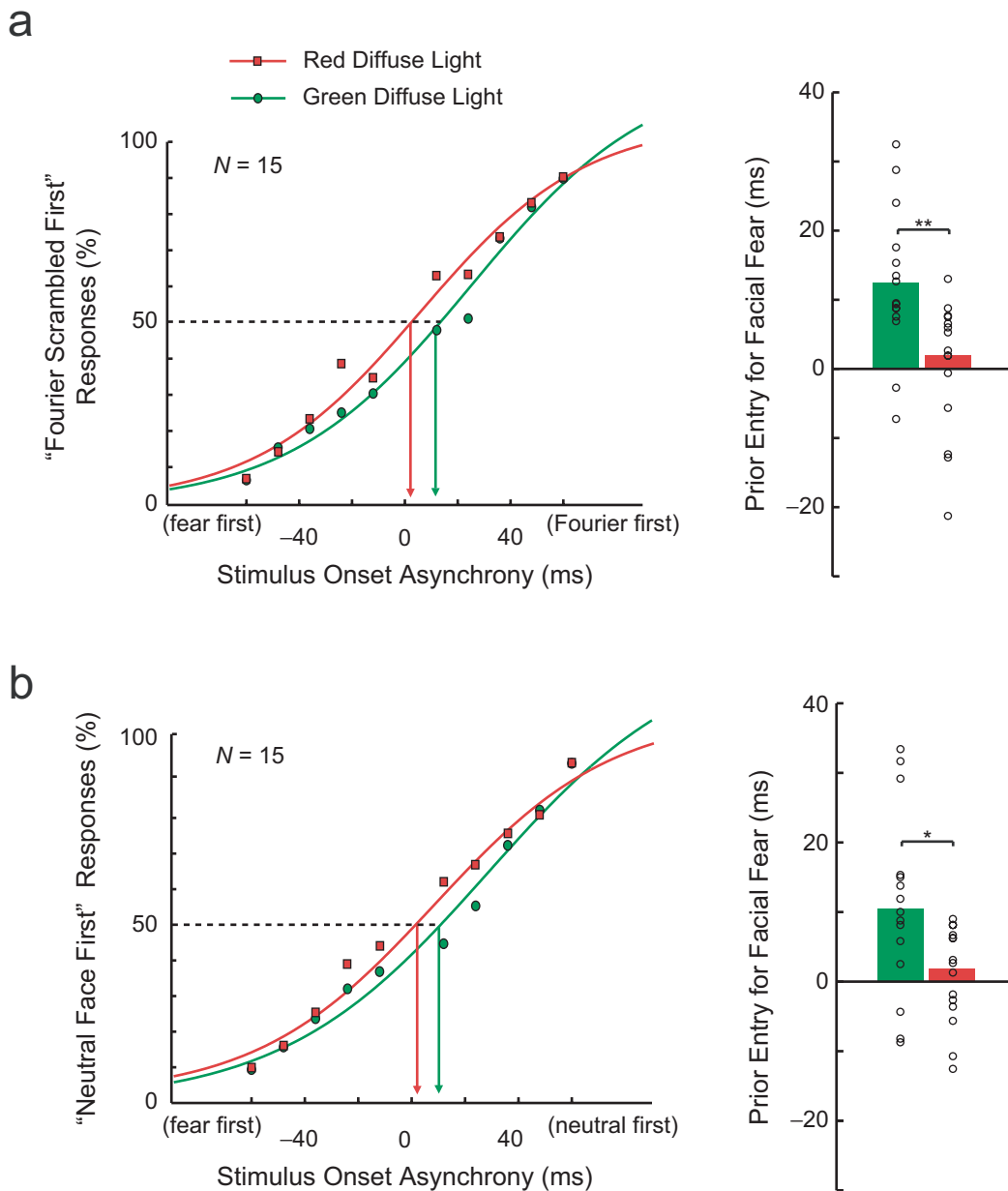


Fig. 3. Results from Experiments 2a and 2b. The graphs on the left present prior-entry psychometric functions for images portraying facial fear. The percentage of responses in which subjects reported (a) a Fourier-scrambled stimulus and (b) a neutral face as having first onset when paired with facial fear is shown as a function of stimulus onset asynchrony (SOA) for conditions of green and red diffuse light. Participants' data were fit to a separate sigmoid function for each lighting condition. Negative SOAs indicate that the fearful face was physically presented first, and positive SOAs indicate that the scrambled or neutral face was physically presented first. The horizontal lines intersecting the curves indicate the point where participants perceived the two stimuli as arriving simultaneously (50%). The arrows represent the temporal value of prior entry; a positive value indicates prior entry for the fearful stimulus, and a negative value indicates prior entry for the scrambled or neutral stimulus. The bar graphs present the average temporal value of perceptual acceleration for the fearful face under the two lighting conditions; individual observers' values are overlaid. The brackets refer to the statistical comparison between conditions (* $p < .05$, ** $p < .01$).

displayed arrow cue that remained on screen for 240 ms before the onset of the two stimuli had a 50% chance of validly predicting the location of the stimulus with the first onset. On the remaining 50% of trials, both line stimuli were presented unilaterally in a single placeholder box, with the arrow cue being 100% valid (so that the arrow cue was overall predictive in the

experiment). Participants reported whether the vertical or horizontal line segment had the first onset. Stimuli remained on screen until participants responded by pressing the “8” key (for “horizontal first”) or the “2” key (for “vertical first”). (The response keys were changed in this experiment to avoid Simon effects.) Only the bilateral trials were included in our analyses

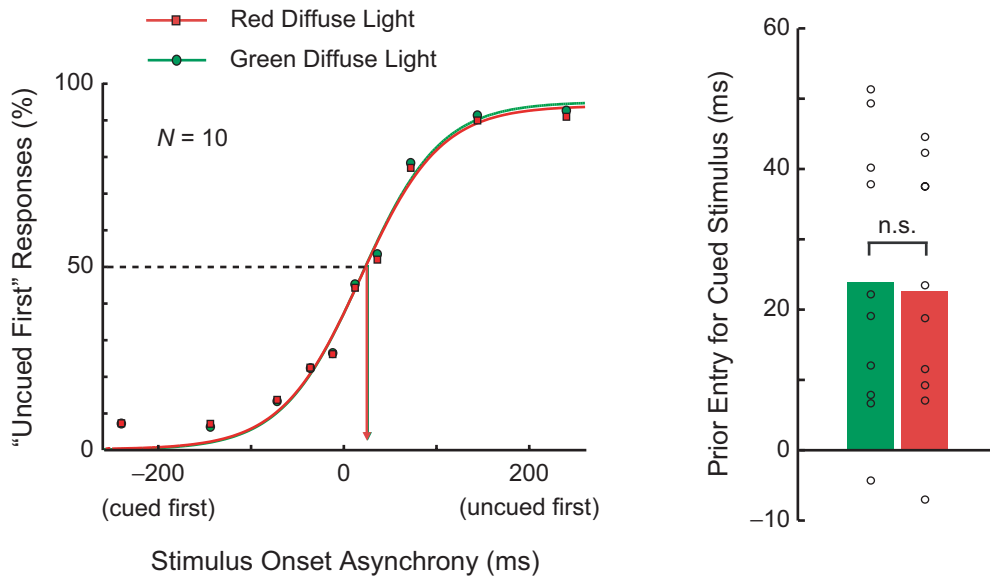


Fig. 4. Results from Experiment 3. The graph on the left presents prior-entry psychometric functions for predictive arrow cuing. The percentage of responses in which subjects reported the uncued stimulus as having first onset is shown as a function of stimulus onset asynchrony (SOA) for conditions of green and red diffuse light. Participants' data were fit to a separate sigmoid function for each lighting condition. Negative SOAs indicate that the cued stimulus was physically presented first, and positive SOAs indicate that the uncued stimulus was physically presented first. The horizontal line intersecting both curves indicates the point where participants perceived the two stimuli as arriving simultaneously (50%). The arrows represent the temporal value of prior entry; a positive value indicates prior entry for the cued stimulus, and a negative value indicates prior entry for the uncued stimulus. The bar graphs present the average temporal value of perceptual acceleration for the cued stimulus under the two lighting conditions; individual observers' values are overlaid. The bracket refers to the statistical comparison between conditions.

(Shore et al., 2001). We used a longer range of SOAs (12, 36, 72, 144, and 240 ms) in this experiment to ensure that there was enough time for top-down bias caused by the arrow cue to take place. Participants completed two separate sessions of 10 blocks, with 60 experimental trials in each block.

Results

The results for Experiment 3, which are summarized in Figure 4, are consistent with accelerated processing as a result of top-down attention. The cued stimulus was perceived on average as arriving 23.88 ms prior to the uncued stimulus under green diffuse lighting, $t(9) = 3.90$, $p < .01$. A similar prioritization of 22.47 ms was found under red diffuse lighting, $t(9) = 4.06$, $p < .01$, with the difference between conditions being nonsignificant ($t < 1$). These results demonstrate a dissociation between perceptual acceleration produced by a top-down bias and perceptual acceleration produced by a stimulus-driven bias, such as that found for facial displays of fear: The former is unaffected by red diffuse light.

Discussion

Facial expressions of fear, like LSF information, are associated with accelerated stimulus perception, being perceived prior to competing stimulus events. Attenuation of M-pathway activity through diffuse red lighting results in the suppression

of these stimulus-driven—but not top-down—sources of accelerated stimulus perception. Thus, perceptual prioritization via M channels may underlie increased subcortical (Rudrauf et al., 2008) and cortical (Anderson, Christoff, Panitz, DeRosa, & Gabrieli, 2003) activity observed in response to displays of facial fear, and possibly mediates other perceptual and attentional benefits associated with fear (Fox, Russo, Bowles, & Dutton, 2001; Phelps, Ling, & Carrasco, 2006). What is it about facial displays of fear that might drive their perceptual prioritization? It has been suggested that information from the eyes and mouth is crucial in the identification of emotional expressions. In the case of facial fear, the increased local contrast in the areas of the eyes and mouth is thought to facilitate their privileged processing (e.g., Schyns, Petro, & Smith, 2009; Whalen et al., 2004). In addition, these physical facial changes associated with fear displays are properties that can be coarsely conveyed through a face's global LSF representation. Because of this LSF-related prioritization, it is possible that facial displays with similar configurations (e.g., surprise) would generate similar prioritization effects, whereas facial displays that decrease relative local contrast around the eye and mouth regions (e.g., disgust) may not enjoy this same privileged status. Continued work on differential prioritization effects surrounding different affective expressions is being conducted to further explore this question.

As retinal M afferents form the dorsal visual pathway primarily responsible for preparatory motor programming

(Goodale & Westwood, 2004; Livingstone & Hubel, 1987), the observed accelerated perception of facial-fear displays via this where-action pathway provides a possible neural mechanism underlying emotion's relationship with action. Prioritized representations of fear might have the ability to modulate motor output both through subcortical M projections involving action-oriented structures, such as the superior colliculus and pulvinar, and through cortical projections involving dorsal parietal structures that influence action programming via feedback loops. Given that M afferents project to neural structures that affect both perception and action, it is possible that fear-based content has the ability to modulate both. This is not a new idea; evolutionary theory has long suggested that emotions originated as adaptations toward action (Darwin, 1872; Frijda, 1986), although this notion has previously had little empirical support. The existence of an expedient prioritization of threat information via the M dorsal action pathway suggests that emotional biases in object perception (Fox et al., 2001; Phelps et al., 2006) may arise from phylogenetically older neural systems specialized for action (Goodale & Westwood, 2004).

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Declaration of Conflicting Interests

The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

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