Low-spatial-frequency information facilitates threat detection in a response-specific manner

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The role of different spatial frequency bands in threat detection has been explored extensively. However, most studies use manual responses and the results are mixed. Here, we aimed to investigate the contribution of spatial frequency information to threat detection by using three response types, including manual responses, eye movements, and reaching movements, together with a priming paradigm. The results showed that both saccade and reaching responses were significantly faster to threatening stimuli than to nonthreatening stimuli when primed by low-spatial-frequency gratings rather than by high-spatial-frequency gratings. However, the manual response times to threatening stimuli were comparable to nonthreatening stimuli, irrespective of the spatial frequency content of the primes. The findings provide clear evidence that low-spatial-frequency information can facilitate threat detection in a response-specific manner, possibly through the subcortical magnocellular pathway dedicated to processing threat-related signals, which is automatically prioritized in the oculomotor system and biases behavior.

Introduction

Fast detection of threats is crucial for survival. This process has been suggested to be facilitated by a rapid and automatic processing of coarse visual features of threatening cues (Lojowska, Mulckhuyse, Hermans, & Roelofs, 2019; Öhman, 2005). For instance, reaction times (RTs) to snake targets were faster than responses to neutral ones (i.e. frogs or rabbits) when stimuli were filtered in low-spatial frequency (LSF) rather than in high-spatial frequency (HSF) (Mermillod, Droit-Volet, Devaux, Schaefer, & Vermeulen, 2010). By using an interocular suppression paradigm, Gomes, Soares, Silva, and Silva (2018) found that snakes took less time than birds in accessing visual awareness when stimuli were filtered in LSF, but not in HSF. Moreover, when participants were in a threat state (i.e. the anticipation of an electric shock), their performance on orientation discrimination of consciously invisible LSF gratings was better than when they were in a safe state. However, the performance advantage in the threat state disappeared for HSF gratings

(Lojowska et al., 2019). Electrophysiological studies have shown that fearful faces elicit faster amygdala responses (i.e. 74-ms post-stimulus onset) than neutral and happy faces when stimuli are filtered in LSF rather than in HSF (Méndez-Bértolo, Moratti, & Toledano, 2016), and such LSF-related threat advantage has been found to be associated with theta power changes within the amygdala (Maratos, Mogg, Bradley, Rippon, & Senior, 2009). An functional magnetic resonance imaging (fMRI) study demonstrates that the amygdala shows increased responses to fearful faces compared to neutral ones for LSF stimuli, but not for HSF stimuli (Vuilleumier, Armony, Driver, & Dolan, 2003). Similar patterns of results have been observed for a patient with bilateral V1 damaged (Burra, Hervais-Adelman, Celeghin, de Gelder, & Pegna, 2017). The prioritized processing of LSF threatening stimuli has been suggested to occur through a fast-acting subcortical pathway originating from magnocellular retinal inputs, which include reciprocal connections between the superior colliculus (SC), the pulvinar, and the amygdala (West, Al-Aidroos, Susskind, & Pratt, 2011).

However, alternative results have also been observed (Aguado, Serrano-Pedraza, Rodríguez, & Román, 2010; Goren & Wilson, 2006; McFadyen, Mermillod, Mattingley, Halász, & Garrido, 2017; Morawetz, Baudewig, Treue, & Dechent, 2011; Ottaviani, Cevolani, Nucifora, 2012; Stein, Seymour, Hebart, & Sterzer, 2014). For example, by using continuous flash suppression and sandwich masking, Stein et al. (2014) found that the threat advantage was specific to HSF instead of LSF fearful faces. Moreover, the amygdala has been found to show comparable responses to LSF and HSF fearful faces (Morawetz et al., 2011) as well as to LSF fearful and neutral faces (Ottaviani et al., 2012) in healthy participants.

The ultimate goal of swift threat detection is to initiate rapid and appropriate responses. The threat advantage has been observed across a variety of response types. For instance, Buetti, Juan, Rinck, and Kerzel (2012) found that, when simultaneously presented a spider and a neutral stimulus, spider-fearful participants reached more directly to the neutral target, and reached less directly to the spider target, compared to controls. Moreover, when presented for a long duration (i.e. 500 ms), fearful faces and bodies elicited faster saccadic and manual responses than neutral ones. However, when presented for a brief duration (i.e. 20 ms), significant threat advantage was observed for saccadic rather than manual responses (Bannerman, Milders, & Sahraie, 2009; Bannerman, Milders, & de Gelder, et al., 2009). Saccades have been suggested to rely more on the faster magnocellular pathway than manual responses (Bompas & Sumner, 2008). Moreover, threatening stimuli have the greatest impact on oculomotor behavior through biased processing via the magnocellular pathway (Mulckhuyse, 2018). Therefore,

we conjecture that the contribution of spatial frequency (SF) to threat detection might vary with response types. To clarify this issue, we adopted a priming paradigm by using LSF and HSF gratings as primes, combined with three response types, including manual responses (i.e. keypresses), eye movements, and reaching movements. Considerable evidence has suggested that the saccadic and reaching systems interact extensively (Gribble, Everling, Ford, & Mattar, 2002; Scherberger, Goodale, & Andersen, 2003; Song & McPeek, 2009). The SC, which is mainly involved in oculomotor behavior, can be selectively activated during visually guided reaches (Himmelbach, Linzenbold, & Ilg, 2013; Stuphorn, Bauswein, & Hoffmann, 2000; Werner, Hoffmann, & Dannenberg, 1997). Therefore, we expected that an LSF-related threat advantage would be more likely observed with saccadic and reaching responses than manual responses.

Methods

Participants

A total of 72 participants (30 men; mean age = 22.54 ± 2.40; age range = 18–28 years) took part in the study, with 24 participants for each of the three experiments. The sample size for this study was determined by computing estimated statistical power ($\beta > 0.9$) using the G*Power (Faul, Erdfelder, Lang, & Buchner, 2007), based on the results of prior experiments on threat advantage (Bannerman, Hibbard, Chalmers, & Sahraie, 2012; Bannerman, Milders, & Sahraie, 2009). They were all right-handed with normal or corrected-to-normal vision, and gave informed consent prior to participating in the study. This protocol was approved by the institutional review board of Liaoning Normal University and adhered to the tenets of the Declaration of Helsinki.

Stimuli

Stimuli were displayed using MATLAB (The MathWorks, Natick, MA, USA) together with the Psychophysics Toolbox extensions (Brainard, 1997; Pelli, 1997). Gabor gratings (5.9 degrees × 5.9 degrees) with cutoffs of one and six cycles per degree were used as primes. The gratings were oriented 45 degrees clockwise or counterclockwise relative to the vertical orientation. Pictures of snakes and spiders (5.9 degrees × 5.9 degrees) were selected from IAPS (Lang, Bradley, & Cuthbert, 1997), and their corresponding scrambled versions were used as a baseline (Figure 1A), according to previous studies (Campbell-Sills, Simmons, Lovero, Rochlin, Paulus, & Stein, 2011; Dinh et al., 2018).
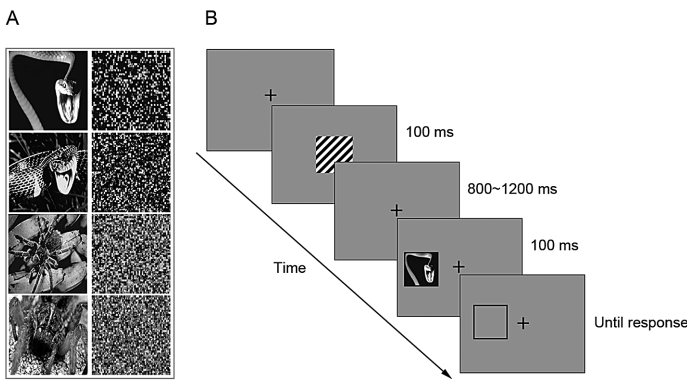
Figure 1. Experimental stimuli and procedure. (**A**) Demonstration of threatening (left column) and nonthreatening (right column) stimuli as used in the study and (**B**) schematic representation of the experimental procedure.

All pictures were assigned identical root mean square contrast and average luminance value using the SHINE toolbox for MATLAB (Willenbockel, Sadr, Fiset, Horne, Gosselin, & Tanaka, 2010). The gratings were displayed at the screen center. The threatening and nonthreatening pictures were presented on either the right or the left of the screen (6.6 degrees from the screen center). Participants were positioned 57 cm from a gray computer screen (gamma corrected, 1280 × 1024 at 60 Hz) with their head positioned on a chin rest.

Procedure

There was a total of 192 trials in each experiment. In each trial, an LSF or HSF grating was presented for 100 ms, followed by a threatening or a nonthreatening stimulus presented on the right or left of the screen for 100 ms (Figure 1B). In experiments 1 and 3, the black frame around the target stimulus would not disappear until the response of participants. In experiment 2, it would be still in situ for 500 ms after the stimulus disappeared. Participants were instructed to passively view gratings, and then to judge the location of the threatening or nonthreatening stimulus relative to fixation point by pressing either the left or right arrow key (experiment 1), by performing an eye movement (experiment 2), or a reaching movement (experiment 3) to the stimulus. In experiments 1 and 3, participants were asked to keep their eyes on the fixation point and press buttons or make reaching movements to the target stimulus as fast as they could. In experiment 2, participants were required to keep their eyes on the fixation point until the target stimulus appeared and then move their eyes as fast as possible to the location of the stimulus.

Eye tracking

Eye movements of the right eye were recorded with EyeLink 1000 plus tracker (SR Research Ltd., Canada) sampling at 1000 Hz with a spatial precision of 0.01 degrees. There was a nine point calibration procedure before the experiment and a drift correction before each trial. Saccades were detected using criteria of the velocity of 30 degrees/second and acceleration of 9500 degrees/second^2. Saccade latency was measured as the time from the onset of the threatening or nonthreatening stimulus until the saccade was initiated.

Reaching task

Participants sat at a table with an LCD touch screen positioned in front of them. Each trial would not start until participants pressed a centrally located button in front of the touchscreen with their right index finger. The starting position was aligned with the body midline and was approximately 30 cm from the body. Participants were required to keep their right index finger on the button before the target onset and use the same finger to reach out and touch the target as soon as the target appeared. Reaching RTs were measured as the time interval between the time of target onset and the time when participants touched the screen.

Statistical analyses

A repeated-measures analysis of variance was conducted with within-subject factors of target type (threatening versus nonthreatening) and SF of gratings (low versus high). Paired-sample *t*-test between threatening and nonthreatening stimulus was adopted to further investigate the threat advantage under each of the SF conditions. Finally, a univariate analysis of variance was used to compare the threat advantage across the three experiments.

Results

In experiment 1, the mean RTs from all trials were collected for further analysis. The results revealed nonsignificant main effects of target type ($F(1, 23) = 1.301$, $p = 0.266$, $\eta_p^2 = 0.054$) and SF of gratings ($F(1, 23) = 0.248$, $p = 0.623$, $\eta_p^2 = 0.011$), as well as a nonsignificant interaction between the two factors ($F(1, 23) = 0.493$, $p = 0.490$, $\eta_p^2 = 0.021$; see Figure 2A). Further analysis showed that manual RTs for threatening stimulus were comparable to nonthreatening stimulus under both LSF
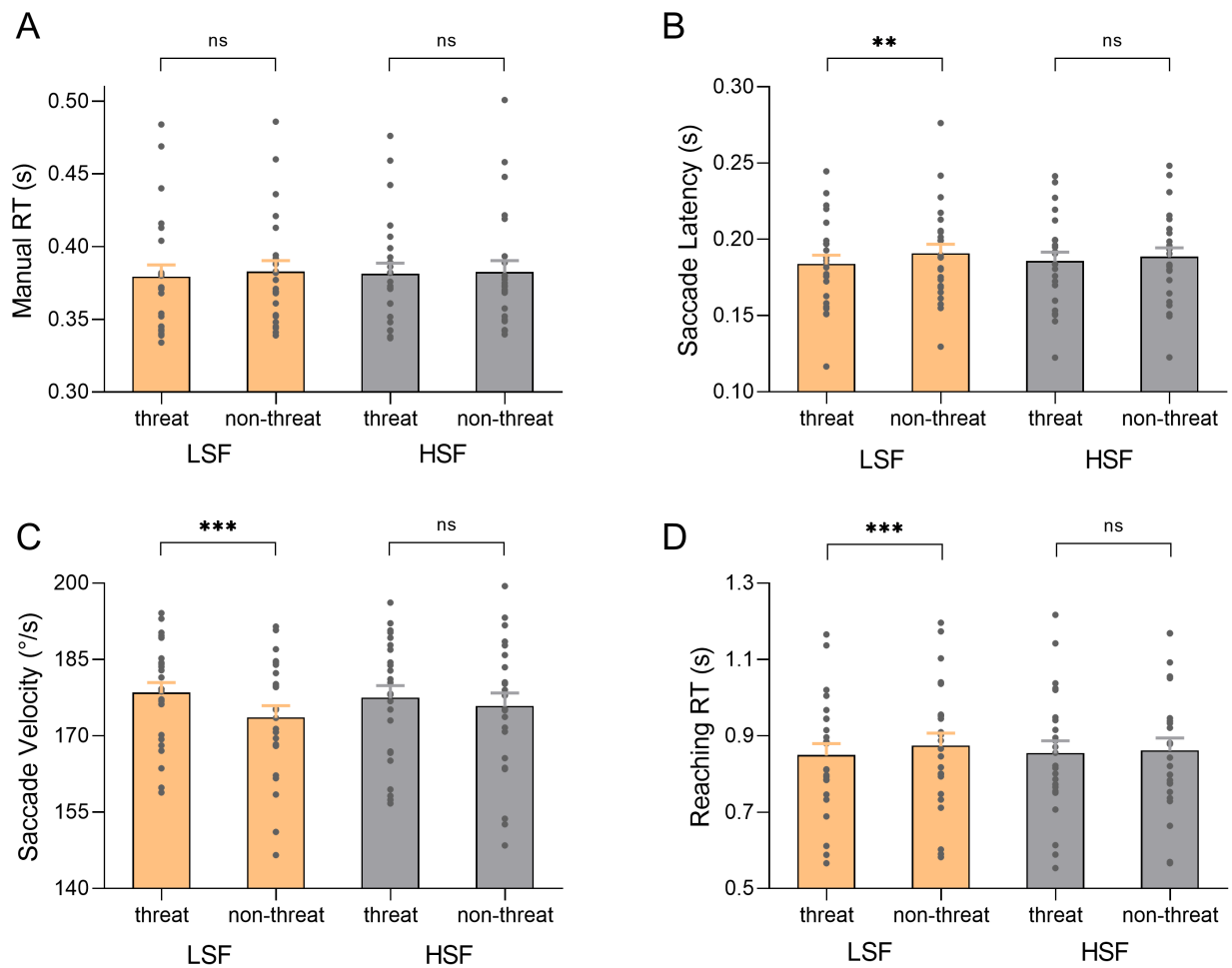
Figure 2. Results of three experiments. (**A**) Manual RTs, (**B**) saccade latency, and (**C**) saccade velocity, as well as (**D**) reaching RTs to threatening and nonthreatening stimuli as a function of spatial frequency. Error bars represent one standard error of the mean. Asterisks (*) indicate a significance level of **$p < 0.01$, and ***$p < 0.001$.

($t(23) = -1.473$, $p = 0.154$, $d = 0.301$) and HSF ($t(23) = -0.372$, $p = 0.713$, $d = 0.076$) conditions.

In experiment 2, trials with saccades faster than 50 ms and slower than 350 ms (1.6% of all trials), and trials with saccade peak velocity slower than 50 degrees/second (0.5% of all trials), as well as trials with the end position of saccades outside the target area (undershoot or overshoot; 9.4% of all trials) were excluded from further analysis. For saccade latency, the main effect of target type was significant ($F(1, 23) = 7.260$, $p = 0.013$, $\eta_p^2 = 0.240$), but the main effect of SF of gratings ($F(1, 23) = 0.005$, $p = 0.945$, $\eta_p^2 = 0.000$) and the interaction between the two factors ($F(1, 23) = 3.496$, $p = 0.074$, $\eta_p^2 = 0.132$) failed to reach significance. Further analysis showed that saccade latency for threatening stimulus was significantly shorter than for nonthreatening stimulus under LSF condition ($t(23) = -2.949$, $p = 0.007$, d

$= 0.602$; see Figure 2B), instead of HSF condition ($t(23) = -1.519$, $p = 0.142$, $d = 0.310$). For average saccade velocity, the main effect of SF of gratings was nonsignificant ($F(1, 23) = 0.489$, $p = 0.491$, $\eta_p^2 = 0.021$), but the main effect of target type ($F(1, 23) = 16.477$, $p < 0.001$, $\eta_p^2 = 0.417$) and the interaction between the two factors ($F(1, 23) = 6.429$, $p = 0.018$, $\eta_p^2 = 0.218$) were significant. Further analysis showed that saccade velocity was significantly faster for threatening stimulus than for nonthreatening stimulus under LSF condition ($t(23) = 4.571$, $p < 0.001$, $d = 0.933$; see Figure 2C), instead of HSF condition ($t(23) = 1.662$, $p = 0.110$, $d = 0.339$).

In experiment 3, the main effect of SF of gratings was not significant ($F(1, 23) = 0.723$, $p = 0.404$, $\eta_p^2 = 0.030$), but the main effect of target type ($F(1, 23) = 9.845$, $p = 0.005$, $\eta_p^2 = 0.300$) and the interaction between the two factors ($F(1, 23) = 7.998$, $p = 0.010$, $\eta_p^2 = 0.258$) were significant. Further analysis showed

that reaching RTs for threatening stimulus were significantly faster than for nonthreatening stimulus under LSF condition ($t(23) = -4.091$, $p < 0.001$, $d = 0.835$; see Figure 2D), instead of HSF condition ($t(23) = -1.190$, $p = 0.246$, $d = 0.243$).

To directly compare the threat advantage ($RT_{non\text{-}threat} - RT_{threat}$) among the three experiments, we log10 transformed the data and calculated the threat advantage for both LSF and HSF conditions. The results showed that the main effect of response type was significant for LSF condition ($F(2, 69) = 3.393$, $p = 0.039$, $\eta_p^2 = 0.090$), but was not significant for HSF condition ($F(2, 69) = 0.451$, $p = 0.639$, $\eta_p^2 = 0.013$). Bonferroni pairwise comparisons revealed that the threat advantage under LSF condition was significantly larger for saccade responses than for manual responses ($p = 0.034$), whereas the threat advantage for reaching responses was comparable to that for saccade responses ($p = 0.746$) and manual responses ($p = 0.466$).

Discussion

The current study investigated the priming effect of SF information on threat detection with three response types, including manual, saccadic and reaching responses. The results revealed that LSF primes significantly facilitated the saccadic responses (i.e. faster saccade velocity) and reaching movements (i.e. faster reaching times) to threatening stimuli compared to nonthreatening stimuli. However, when participants were required to make manual responses to the stimuli, the LSF-related threat advantage disappeared. Moreover, with HSF primes, the threat advantage was not observed in any of the three response types. The findings suggest that the contribution of SF to threat detection varies with response types, with the LSF-related threat advantage being more likely observed with saccadic and reaching responses than manual responses.

Converging evidence has demonstrated an automatic attentional capture by threatening compared to nonthreatening stimuli. In particular, threat-relevant targets were detected more quickly than threat-irrelevant ones (Flykt, 2005; Ohman, Flykt, & Esteves, 2001). The detection of a target is faster when primed by threat-related cues in comparison with neutral cues (Bannerman, Milders, & Sahraie, 2010; Koster, Crombez, Van Damme, Verschuere, & De Houwer, 2004; Koster, Crombez, Verschuere, Vanvolsem, & De Houwer, 2007). Moreover, when face stimuli were rendered consciously invisible with continuous flash suppression, participants moved their eyes toward fearful faces compared to neutral faces (Vetter, Badde, Phelps, & Carrasco, 2019). Furthermore, fearful faces

elicited shorter saccade latencies compared to neutral and happy faces when the face stimuli were filtered in LSF rather than in HSF (Bannerman et al., 2012). In line with and extending the aforementioned evidence, the current study showed that threatening stimuli elicited faster saccadic and reaching responses than nonthreatening stimuli. Notably, the threat advantage was observed when primed by an LSF rather than an HSF grating. Three possible pathways by which the amygdala may modulate the oculomotor behavior have been proposed (Mulckhuyse, 2018). One is through a subcortical loop involving the SC, the pulvinar, and the amygdala, and the other two are through cortical connections with either the visual cortex or the frontal areas projecting back to the SC. Our findings lend support to the rapid subcortical pathway by showing that significant threat advantage upon the fast saccadic and reaching movements was observed in LSF instead of HSF channels.

The preparation and execution of saccades and reaching movements elicit an accompanying attentional shift at the locus of the impending movement (Stewart, Verghese, & Ma-Wyatt, 2019). Inconsistent findings have been reported regarding whether the attentional systems underlying target selection for eye and reaching movements are separate or shared. For instance, by asking participants to perform simultaneous eye and reaching movements to separate locations, it has been found that performance at the saccade location was unaffected by a simultaneous reaching movement to another location, and performance at the reaching location was unaffected by a simultaneous saccadic movement to another location, suggesting that an independent, effector-specific attentional mechanisms are involved in selecting saccade and reach targets (Hanning, Aagten-Murphy, & Deubel, 2018; Jonikaitis & Deubel, 2011). Neuroimaging studies have identified distinct parietal regions that show preparatory activity before eye or reaching movements (Tosoni, Galati, Romani, & Corbetta, 2008; Van Der Werf, Jensen, Fries, & Medendorp, 2010). However, Nissens and Fiehler (2018) have found that when planning simultaneous eye and reaching movements, the movement trajectory of one effector curves away and its end point is shifted away from the other effector's target location, suggesting a shared attentional system involved in selecting saccade and reach targets. Moreover, by using an exogenous cueing paradigm, Malienko, Harrar, and Khan (2018) have found no difference of response amplitudes and RTs between single and combined movements for both saccade and reaching movements. Furthermore, the present study showed that both saccade and reaching responses were significantly faster to threatening stimuli than to nonthreatening stimuli when primed by an LSF rather than by an HSF grating. Neuroimaging studies have found an overlap of the systems involved in selecting eye and

reaching movements in both parietal and prefrontal cortex (Beurze, De Lange, Toni, & Medendorp, 2009; Levy, Schluppeck, Heeger, & Glimcher, 2007), as well as the SC (Gandhi & Katnani, 2011; Krauzlis, Lovejoy, & Zénon, 2013; Lünenburger, Kleiser, Stuphorn, Miller, & Hoffmann, 2001). Therefore, the current study supports a shared attentional system underlying saccade and reaching movements and suggests that both might receive magnocellular projections from the subcortical visual pathway that conveys LSF information.

Manual responses have been suggested to involve distinct neural processing compared to eye and reaching movements. For instance, the RT advantage of luminance stimuli relative to S-cone stimuli was significantly larger for saccadic than for manual responses, and no significant correlation was found between saccadic and manual responses in terms of the RT advantage, suggesting that saccades rely more on the fast magnocellular pathway than manual responses (Bompas & Sumner, 2008). Eye movements are a more direct and naturalistic measure of attention capture relative to manual responses (Bannerman et al., 2012), and are typically elicited faster than manual responses (Bannerman et al., 2010). Moreover, the dominant mechanism for direct reaching responses is thought to be visual spatial attention, whereas the dominant mechanism for indirect and arbitrary keypress responses is effector selection (Adam, Taminiau, & van Veen, 2008; Adam & Pratt, 2004; Buetti & Kerzel, 2010). Therefore, in the current study, the disappearance of the LSF-related threat advantage for manual responses might be due to the fact that manual responses were less sensitive than saccade and reaching movements to the attention captured by threat signals, which are mainly conveyed by LSF channels.

The results we obtained are not likely attributed to the difference of the spatial frequency spectra between intact and scrambled images. Bruchmann, Schindler, and Straube (2020) investigated the effect of spatial frequency spectra on the processing of facial expressions (fearful versus neutral). They manipulated the spatial frequency spectra of face images to contain either the average power spectra of neutral, fearful, or both expressions combined. They found that the spatial frequency spectra of fearful faces modulated the amplitude of P1, which is associated with low-level physical features, rather than the amplitude of N170, which is associated with threat-related expressions including fearful faces. Their findings indicate that low-level spatial frequency spectra have a negligible effect on the processing of fearful expression. Moreover, in our study, we adopted a priming paradigm, in which the SOA between the prime and the target was 900 to 1300 ms. Thus, the priming effect was not likely caused by low-level spatial frequency spectra. Further, the target was presented for a relatively short duration (i.e. 100 ms), and the mean saccade latency was the fastest,

and the mean reaching RT was the slowest. If low-level spatial frequency spectra do have an effect on the results, it should have the most effect on saccade response, the moderate effect on manual response, and the least effect on reaching response. However, our results showed significant interaction of target type (threatening versus nonthreatening) and SF of gratings (low versus high) for both saccade and reaching responses, but not for manual response.

Conclusion

By using a priming paradigm, the current study showed significant LSF-related facilitation of threat detection for saccadic and reaching movements, rather than manual responses. The findings provide direct evidence that LSF information can facilitate threat detection in a response-specific manner, possibly through the subcortical magnocellular pathway dedicated to processing threat-related signals, which is automatically prioritized in the oculomotor system and biases behavior. Further studies are needed to measure reach latency in order to better compare with saccade latency and manual responses.

Keywords: threat, spatial frequency, manual responses, saccade, reaching

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