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Increased inhibition following negative cues: A possible role for enhanced processing

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ABSTRACT

Based on findings showing that attention is captured by aversive stimuli, previous studies have hypothesized that inhibition of return (IOR) is reduced at spatial locations previously occupied by threat cues. Yet evidence for this view is limited: Only a few studies have demonstrated a reduced degree of IOR following threat cues, while most have not found differences in IOR between aversive and neutral cues. In contrast to previous studies that used the spatial cuing paradigm and for the most part employed mild negative stimuli as cues, we examined the influence of highly aversive, colored and complex pictures of real life situations. As opposed to the stimuli used in previous studies, these pictures are thought to result in enhanced processing as well as in specific enhancement for threat pictures in comparison to neutral ones. Based on evidence indicating that enhanced processing of spatial cues results in increased IOR, we hypothesized that the negative picture cues employed in the present study would yield increased IOR. This hypothesis was confirmed in two experiments. We suggest that the enhancement of IOR following highly threatening cues may be related to efficient spatial orienting of attention in response to stimuli that are important from an evolutionary point of view. The results are discussed in the context of neurocognitive mechanisms that may underlie the modulation of IOR by emotional information.

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1. Introduction

Human beings are exposed to more external and internal stimuli than our attentional system can process (Yantis, 1996). Therefore, certain stimuli, such as those that are threat related, are prioritized based either on their evolutionary value or on current goals (see review in Okon-Singer, Lichtenstein-Vidne, & Cohen, 2013). Prioritized processing of negative stimuli has been demonstrated by showing the influence of threat distractors on performance in a competition task. For example, when participants were asked to respond according to a target letter while ignoring distracting pictures, they nevertheless responded more slowly when presented with a distracting task-irrelevant negative picture but not when the distracting picture was neutral (Okon-Singer, Tzelgov, & Henik, 2007, 2014).

Differential processing of threat stimuli was also demonstrated by differences in the allocation of attention to threat cues compared to cues that are not threatening (for discussion see Aue & Okon-Singer, 2015). For example, in the dot-probe task commonly employed to examine the allocation of spatial attention to emotional cues, two stimuli appear briefly: an emotional cue and a neutral cue. Participants are asked to respond according to a dot-probe that appears either at the location of the emotional cue or at the location of the neutral cue (MacLeod, Mathews, & Tata, 1986). While evidence indicates that participants respond faster to probes appearing at the location of the emotional cues than to those appearing at the neutral cue locations, many have failed to replicate this finding (see discussion in Okon-Singer, 2018). Researchers interpreted the facilitation of responses at emotional locations as representative of difficulty in disengaging attention from an emotional cue (Koster, Crombez, Van Damme, Verschuere, & De Houwer, 2004). This interpretation is based on the view that orienting attention involves disengaging attention from its current location, moving it to a new location and engaging it there (Posner, Walker, Friedrich, & Rafal, 1984).

Another task used to examine how attention is allocated to threat stimuli is the spatial cuing task (Posner, 1980). In the exogenous version of this task, a spatial cue reflexively attracts attention to its location. Following a certain stimulus onset asynchrony (SOA), a target appears at the cued or the opposite location. In the classic task, reaction times (RTs) at short SOAs are usually shorter when the target appears at cued locations (i.e., valid trials). In contrast, with longer SOAs, RTs are faster at the non-cued location (i.e., invalid trials). This finding with longer SOAs is termed inhibition of return (IOR) and is commonly explained by the *reorienting* theory. According to this theory, once attention is engaged at a cued location, an inhibitory process emerges to facilitate the processing of new locations in the visual field (Klein, 2000).

As noted, several studies have examined the presentation of emotional cues in the spatial cuing paradigm and have yielded mixed findings (see below). Emotional cues are assumed to be subject to enhanced processing due to their higher arousal levels compared to neutral cues (Lang, Greenwald, Bradley, & Hamm, 1993; see review in; Okon-Singer et al., 2013). The impact of a cue's level of processing on the inhibitory effect has been debated in the literature discussing the spatial cuing paradigm. According to one view, inhibition is apparent mostly after disengagement from the cued location. Hence, stimuli that attract attention to a greater extent and require enhanced processing should delay disengagement and reduce or delay the appearance of inhibition (Klein, 2000). Accordingly, if an emotional stimulus attracts more attention and is subject to enhanced processing, it should produce larger facilitation and delayed/reduced IOR (Berdica, Gerdes, & Alpers, 2017). This view is similar to the interpretation of the findings of the dot-probe task, according to which orienting attention involves disengaging, moving and engaging attention from one location to another. According to this view, difficulty in disengaging attention from a specific location should produce a larger facilitation effect.

In contrast, according to an alternative interpretation of the influence of cue level processing on attentional effects, enhanced processing of a spatial cue may actually result in increased IOR. In one study, Gabay, Chica, Charras, Funes, and Henik (2012) used a spatial cuing task to examine the influence of processing demands on IOR by independently manipulating the processing level of cue and target. Participants were required either to discriminate or to localize the target. In addition, at the end of each trial participants were asked to answer a yes/no question regarding the identity (discrimination) or location (localization) of the cue. The results demonstrated that discrimination of the cue or target, which requires enhanced processing, produced a larger IOR effect than did indicating the location of the cue or target (Gabay et al., 2012). Another study employed pupilometry measurements during Posner's cuing task (Gabay, Pertzov, & Henik, 2011). In this study, larger pupil size, which is indicative of norepinephrine release and enhanced alertness, was correlated with increased IOR. Based on these findings it is plausible to hypothesize that emotional cues, which are known to elicit high arousal, will result in enhanced IOR.

As noted, several studies used emotional stimuli as cues in the spatial cuing paradigm, yielding mixed results. According to the first view hypothesizing delayed disengagement from threat cues, short SOAs combined with threat cues should result in smaller IOR than with neutral cues (e.g., see hypothesis in Berdica et al., 2017). Yet while a few studies indeed showed slower RTs following negative—as opposed to neutral—cues (e.g., Bertels, Kolinsky, Bernaerts, & Morais, 2011; Fox, Russo, & Dutton, 2002; Koster et al., 2004; Pan, Wu, Zhang, & Ou, 2017; Pérez-Duenas, Acosta, & Lupiáñez, 2014; Shang, Huang, & Ma, 2015), other studies failed to find differences between negative and neutral cues (e.g., Berdica et al., 2017; Hu, He, Fan, & Lupiáñez, 2014; Stoyanova, Pratt, & Anderson, 2007). In contrast, Stormark and Hugdahl (1996) showed increased IOR following highly aversive cues, in line with the view that enhanced alertness results in greater inhibition.

How do these studies differ? While Stormark and Hugdahl presented participants with cues that had been conditioned to an aversive noise, other researchers used schematic drawings of biological threats, negative words, black and white pictures or face pictures as cues. Previous studies have shown that allocation of attention toward negative stimuli is modulated by features of the stimulus, as well as to the context and relevance of the stimulus to the participant (Aue & Okon-Singer, 2015; Lichtenstein-Vidne, Henik, & Safadi, 2012; Okon-Singer, 2018; Okon-Singer et al., 2013). Stimuli that participants do not find highly arousing may not affect how they orient attention toward these stimuli, especially when the stimuli are irrelevant to the task (for elaboration see Lichtenstein-Vidne et al., 2017; Okon-Singer et al., 2011;Okon-Singer et al., 2014). Fear-conditioned stimuli are considered highly aversive and are known to result in stress responses, high sympathetic arousal (Lang et al., 1993) and norepinephrine release (Díaz-Mataix et al., 2017). According to Gabay et al. (2011), such highly arousing cues should result in increased IOR.

To summarize, two different theoretical accounts have been proposed. According to one theory, IOR will be reduced following negative cues due to enhanced engagement and difficulty in disengagement from the cued location. In contrast, a second theory posits that IOR will be enhanced following negative cues due to enhanced processing and higher arousal value. To explore these two theoretical accounts, we conducted two experiments to examine how highly aversive cues modulate the distribution of exogenous attention in healthy individuals. Contrary to previous studies, we used highly arousing, negative, real-life colored pictures as exogenous cues that did not predict the location of the target. In Experiment 1, we employed a between-subject design in order to avoid any long-lasting after-effects of the emotional cues on the neutral and scrambled cues. Experiment 2 used a within-subject design in order to replicate the findings and verify that they were not due to individual differences or accumulation of the emotional response.

2. Experiment 1

To examine the impact of emotional cues, we used the exogenous version of the Posner cuing task with highly arousing negative picture cues. We used several SOA durations to avoid expectancy effects as well as to explore the time course of IOR. Based on previous literature regarding the facilitated processing of negative stimuli (e.g., Pourtois, Spinelli, Seeck, & Vuilleumier, 2010), we expected that emotional effects would emerge already at an early SOA. Four different SOA durations were used in random order (100 msec, 400 msec, 700 msec, 1,000 msec). In order to control for confounding effects of visual properties, we also presented scrambled versions of the negative pictures in addition to the negative and neutral pictures. These pictures were similar to the negative items in their visual properties. We hypothesized that negative cues would elicit greater IOR than would neutral or scrambled cues.

2.1. *Method*

2.1.1. *Participants*

Forty-two students from Ben-Gurion University of the Negev participated in the experiment in exchange for course credit. Participants were randomly divided into three separate groups according to cue type presented (negative, neutral, scrambled). All the participants had correct or corrected vision and had no neurological or psychiatric history. The experiment was approved by the local ethics committee.

2.1.2. *Apparatus and stimuli*

Pictures were adapted from the International Affective Picture System (IAPS; Lang, Bradley, & Cuthbert, 2001). The IAPS is a large set of standardized, ecological and emotionally evocative color photographs covering a wide range of categories. The IAPS was developed to provide researchers around the world with a set of normative emotional stimuli for experimental investigations of emotion and attention. Each picture was normatively rated in the US in terms of valence (ranging from pleasant to unpleasant), arousal (ranging from calm to excited) and dominance (ranging from in control to dominant). These three dimensions are considered to be good dimensions for evaluating and defining emotions, with the first two dimensions (i.e., valence and arousal) considered the primary dimensions. These affective judgments of valence, arousal and dominance have high internal consistency (i.e., have high split-half correlation and are replicable across studies) and exhibit high correlations when using several behavioral and physiological measures of emotion (i.e., the self-assessment manikin rating, the semantic differential scale rating, muscle tonus, heart rate and skin conductance; Bradley & Lang, 1994; Greenwald, Cook, & Lang, 1989; Lang et al., 1993). The pictures used in the current study were chosen based on a validation experiment conducted among a sample of young Israeli adults (Okon-Singer et al., 2007). The negative pictures included pictures of mutilated bodies, weapons, violent situations and threatening animals. The neutral pictures included pictures of landscapes, objects, non-emotional social events. The scrambled pictures were created from the negative pictures set. Forty-eight pictures from each category were presented. The stimuli were shown on a black background, and consisted of a fixation dot (.7°) at the center of the computer screen, after which three square boxes (9.5° width, 7.5° height) appeared, one centered on the screen and the other two centered 7.5° to the left and right of the outer edge of the central square. The cue picture appeared at the center of one of the peripheral boxes, followed by a target asterisk (1.5°) that appeared at the center of one of the peripheral boxes.

2.1.3. *Procedure*

In all groups, participants identified the target by pressing the spacebar on a keyboard. The cue picture was not predictive regarding target location. Each participant underwent 432 trials, divided over three experimental blocks of 144 trials each, of which 16 were catch trials (in which no target appeared). Each block included four different SOAs (100 msec, 400 msec, 700 msec, 1,000 msec) and two validity conditions (valid, invalid) that were presented in random order. Prior to the experimental blocks, participants participated in 18 practice trials.

Participants were tested in a dimly illuminated room. They were seated 57 cm from the computer monitor and instructed to maintain fixation throughout the experiment. They were informed that the cue picture was not informative regarding target location and were asked to respond as quickly as possible when the target asterisk appeared. Each trial began with the appearance of a fixation dot for 500 msec. Two hundred ms after the fixation disappeared, a cue appeared for 100 msec. After a SOA (which varied in duration), the target asterisk appeared for 2,500 msec or until response. This was followed by a blank screen appearing for 1,500 msec, after which the next trial started.

2.2. Results and discussion

Trials in which RTs were faster than 100 msec and trials differing by more than two standard deviations from the averaged RT for the specific participant and experimental condition were excluded from the analyses (in total, 2.5% of the trials were excluded).

An analysis of variance (ANOVA) was conducted, with cue type (negative, neutral, scrambled), SOA (100 msec, 400 msec, 700 msec, 1,000 msec), and validity (valid, invalid) as the variables (see Table 1). Fig. 1 shows RTs as a function of validity for each experimental group. Main effects were found for SOA (faster RTs for longer SOAs) and validity (faster RT for invalid trials than for valid trials), F (3, 117) = 97.5, $p < .001$, $n^2p = .71$, and F (1, 39) = 250, $p < .001$, $n^2p = .86$, respectively. The main effect of SOA was examined to verify whether it existed across all SOAs, yielding a linear trend, F (1, 39) = 61.6, $p < .001$, $n^2p = .61$. The interaction between SOA and validity was significant, F (3, 117) = 27, $p < .001$, $n^2p = .41$. This interaction emerged from a larger IOR effect at the averaged two first SOAs compared to the averaged later two SOAs, F (1, 39) = 34.5, $p < .001$, $n^2p = .46$. It should be noted that the two-way interaction between cue type and validity was also significant, F (2, 39) = 3.3, $p < .05$, $n^2p = .14$, showing that negative cues yielded a bigger IOR compared to the two other cue types, F (1, 39) = 6.7, $p < .05$, $n^2p = .14$, while no difference emerged between neutral and scrambled cues, F (1, 39) < 1, *ns*; Fig. 1. The three-way interaction between cue type, validity and SOA was not significant, F (6, 117) < 1, *ns*, indicating that this difference was not modulated by SOA. As we aimed to reveal the time course of IOR modulation, we further explored the three-way interaction. We compared the negative and average IOR effects for the other two conditions at short SOAs (averaged first two SOAs) and at long SOAs (averaged last two SOAs). These comparisons were both significant, F (1, 39) = 4.9, $p < .05$, $n^2p = .11$, and F (1, 39) = 5.2, $p < .05$, $n^2p = .11$, respectively, indicating that the influence of emotional cues was not restricted to early SOAs but also emerged at longer SOAs. We also conducted similar comparisons between the neutral and scrambled conditions, which were not significant; $F < 1$ for both comparisons.

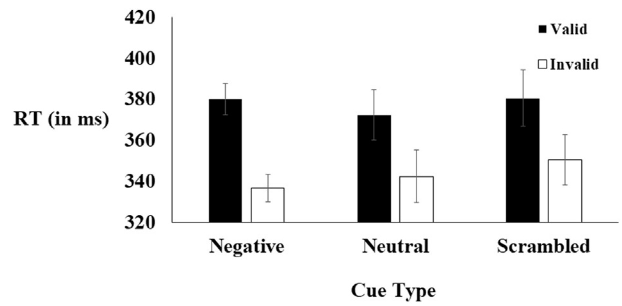

Fig. 1 – Larger IOR effect [i.e., reaction time (RT) of valid minus invalid trials] with negative cues than with neutral or scrambled cues. The size of the IOR effect was similar following neutral and scrambled cues. Error bars denote standard error of the mean (SEM) across participants.

In summary, the results of Experiment 1 are in line with the view that increased IOR emerges due to enhanced processing of exogenous spatial cues (Gabay et al., 2012; 2011). Note, however, that the IOR magnitude at the 100 msec SOA in Experiment 1 was greater than the known IOR magnitude found in previous studies (~40 msec; e.g., Klein, 2000). This result may be due to the visual properties of the cues employed (i.e., large colorful images compared to the usual subtle change in brightening employed as a cue). The largest IOR effect was observed following negative cues, due to their threat value. In addition, as was previously demonstrated, enhanced processing of the cue produced IOR at early SOAs (i.e., 100 msec; Gabay et al., 2012). Nevertheless, since the cues were presented in a between-subject fashion, it is impossible to rule out general mood differences that may have affected the participants' behavior prior to cue onset. The presentation of negative pictures may have induced a negative mood in this group, which may have led to more general attentional effects. We were interested in the phasic attentional effects of the threat cues. For this reason, and in order to verify that the increased IOR demonstrated in this experiment was due to the cue rather than to general differences in mood, we employed a within-subject design in the second experiment. Furthermore, we added a condition of a bright cue that resembled the classic cuing paradigm in order to compare our findings to customary findings.

3. Experiment 2

Experiment 2 was identical to the first experiment except for the use of a within-subject design and the addition of a control

Table 1 – Reaction time for every experimental condition in Experiment 1.

Cue type	SOA							
	100		400		700		1,000	
	Invalid	Valid	Invalid	Valid	Invalid	Valid	Invalid	Valid
Negative	359 (27)	420 (30)	321 (25)	360 (29)	325 (30)	358 (36)	334 (29)	370 (31)
Neutral	374 (50)	425 (48)	327 (46)	356 (45)	336 (52)	355 (44)	342 (56)	364 (59)
Scrambled	382 (44)	429 (53)	343 (51)	368 (54)	345 (49)	372 (56)	355 (51)	381 (50)

Note. RT in milliseconds. Standard deviation in parentheses. SOA – stimulus onset asynchrony.

no-picture cue (the brightening of a peripheral box). We hypothesized that IOR would be larger following negative cues than following neutral, scrambled and no picture cues.

3.1. Method

3.1.1. Participants

Twenty students from the University of Haifa participated in the experiment in exchange for course credit. All the participants had correct or corrected vision and had no neurological or psychiatric history. The experiment was approved by the local ethics committee. One participant was excluded due to high variance in RTs (higher than 2.5 SD from the sample), resulting in a sample of 19 participants.

3.1.2. Apparatus and stimuli

All stimuli were identical to those in the first experiment. In addition to the negative, neutral and scrambled images, we also used a standard exogenous cue that was created by changing the width of one of the peripheral boxes from 1 to 5 mm.

3.1.3. Procedure

All the participants identified the target by pressing the spacebar on a keyboard. The cue picture was not predictive of target location. Each participant underwent 532 trials, divided over two experimental blocks of 266 trials each, of which ten were catch trials (in which no target appeared). Each block contained four different cue types (negative, neutral, scrambled, brightening), four SOAs (100 msec, 400 msec, 700 msec, 1,000 msec) and two validity conditions (valid, invalid), presented in random order. Prior to the experimental blocks, participants performed 18 practice trials.

Participants were tested in a dimly illuminated room. They were seated 57 cm from the computer monitor. Participants were instructed to maintain fixation throughout the experiment. They were informed that the cue was not informative regarding target location and were asked to respond as quickly as possible when the target asterisk appeared. Each trial began with the appearance of a fixation dot for 500 msec. Two hundred ms after the fixation dot disappeared, a cue appeared for 100 msec. After a SOA that varied in duration, the target asterisk appeared for 2,500 msec or until response. This was followed by a blank screen that appeared for 1,500 msec, after which the next trial began.

3.2. Results and discussion

Trials in which RTs were faster than 100 msec and trials that differed by more than two standard deviations from the average RT for a specific participant and experimental condition were excluded from the analyses (in total, 4.5% of the trials were excluded).

An ANOVA was conducted with cue type (negative, neutral, scrambled, brightening), SOA (100 msec, 400 msec, 700 msec, 1,000 msec), and validity (valid, invalid) as the variables. Fig. 2 shows RTs as a function of validity for each experimental group. Table 2 depicts the RTs in the different experimental conditions. Main effects were found for SOA [RT declined as SOA increased, as indicated by a significant linear trend, F (1, 18) = 78.7, $p < .001$, $n^2p = .81$], and for validity (faster RT for invalid trials than for valid trials), F (3, 54) = 57.9, $p < .001$, $n^2p = .76$, and F (1, 18) = 5.3, $p < .05$, $n^2p = .22$, respectively. Only the interaction between cue type and validity reached significance, F (3, 54) = 27, $p < .001$, $n^2p = .26$. In order to assess the emotional effect of the cue, we compared the negative and neutral conditions. As expected, negative cues produced a larger IOR effect, F (1, 18) = 9.1, $p < .01$, $n^2p = .33$. We also sought to examine whether the presence of a cohesive visual image might influence IOR. We tested this by comparing the neutral and scrambled conditions, which did not differ, F (1, 18) = 1.7, *ns*. We also examined the influence of the visual properties of our image cues by comparing the scrambled and brightening conditions. Scrambled cues produced a larger IOR than did brightening of the peripheral box, F (1, 18) = 7.5, $p < .05$, $n^2p = .29$.

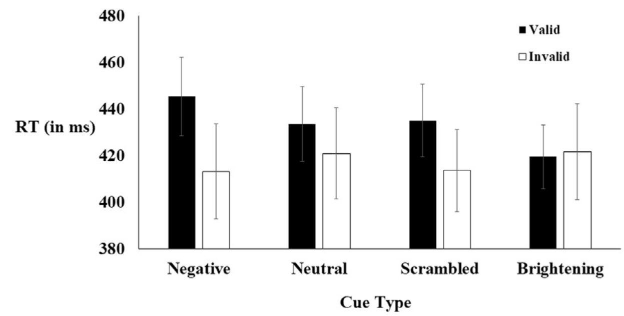

Fig. 2 – Larger IOR effect [i.e., reaction time (RT) of valid minus invalid trials] for negative cues than for neutral, scrambled or brightening cues. Error bars denote standard errors of the mean (SEM) across participants.

The findings of this experiment corroborate those of Experiment 1 and support the view that enhanced processing of highly arousing negative cues yields larger IOR. Replication of the findings in a within-subject design demonstrates that the results are due to the phasic influence of the negative cue on attention orienting and are not the result of a general negative mood throughout the experiment. Control conditions demonstrated that the findings emerged from the negative arousing content and not from sensory visual features or processing of any visual content. Furthermore, replication of the findings in both between- and within-subject designs highlights their reliability over and above specific factors related to the experimental design.

4. General discussion

In the current study we used a spatial cuing task to demonstrate that highly arousing exogenous threat cues yield larger IOR than do neutral, scrambled or perceptual control cues. Experiment 1 used a between-subject design in order to avoid long-lasting within-subject effects of the negative cues on the reaction to neutral and scrambled cues. The findings were replicated in a within-subject event-related design in Experiment 2, demonstrating that the effects emerge from the phasic influence of the threat cues on attention orienting and not from general negative mood or individual differences.

Table 2 – Reaction time for every experimental condition in Experiment 2.

Cue type	SOA							
	100		400		700		1,000	
	Invalid	Valid	Invalid	Valid	Invalid	Valid	Invalid	Valid
Negative	476 (117)	506 (82)	391 (74)	415 (61)	392 (106)	431 (75)	395 (79)	430 (98)
Neutral	465 (84)	494 (81)	395 (71)	413 (66)	411 (115)	417 (83)	413 (104)	411 (71)
Scrambled	467 (84)	481 (66)	405 (90)	413 (69)	388 (77)	417 (91)	395 (80)	429 (69)
Brightening	473 (104)	461 (71)	403 (73)	388 (50)	400 (93)	411 (72)	411 (111)	418 (72)

Note. RT in milliseconds. Standard deviation in parentheses. SOA – stimulus onset asynchrony.

The results of the current study support the notion that highly arousing emotional cues elicit enhanced IOR. This result may be due to the avoidance of spatial locations associated with threat or to enhanced processing and higher arousal elicited by the cue. In accordance with our previous research (Gabay et al., 2012; 2011), we suggest that the second explanation can account for the current findings as well as for evidence of larger IOR following enhanced processing of non-threatening cues due to task demands or high arousal levels during cue processing. In previous studies when participants were asked to report the identity of a cue (i.e., a difficult task resulting in enhanced processing of the cue), IOR was greater than in a condition in which participants had to report the cue location (i.e., an easier task resulting in reduced processing of the cue). Similarly, we previously showed that the levels of cue processing and of arousal, as assessed by pupil size time-locked to cue appearance, correlated with the magnitude of IOR. As noted, threat information results in high arousal as well as prioritized and enhanced processing compared to what is elicited by neutral information (Phan, Wager, Taylor, & Liberzon, 2002). The current findings suggest that this enhanced processing leads to enhanced inhibition of locations occupied by negative stimuli, similar to other cues that are subject to enhanced processing. From an evolutionary perspective, like other cues that are prioritized due to task demands and receive enhanced processing, negative stimuli also elicit efficient searching of the environment. Thus IOR may be initiated as a mechanism that facilitates efficient visual search in the face of threat.

We propose that the magnitude and time course of IOR are modulated by the functioning of the locus coeruleus-norepinephrine (LC-NE) system. Previous studies employing behavioral manipulations and pupil size measurements to index LC-NE activity have indicated that changes in IOR magnitude and time course can be accounted for by changes in LC activity. Specifically, it has been suggested that the LC-NE system has two modes of activity—tonic and phasic (for a review see Aston-Jones & Cohen, 2005). The tonic-firing mode is effective during exploration for new rewards. In contrast, the phasic-firing mode causes specific activation for targets that are rewarding but not for those that are distracting. This suggestion is in line with the arousal-based competition (ABC) view, according to which emotional cues increase arousal and lead to biased orienting of attention toward task-relevant cues and away from task-irrelevant information (Mather, Clewett, Sakaki, & Harley, 2016; Mather & Sutherland, 2011). The phasic and tonic firing modes of the LC-NE system have been suggested to account for differences in the time course and magnitude of IOR in different tasks (Gabay & Henik, 2010; Gabay et al., 2011; Gabay et al., 2012). We suggest that the present results are indicative of the influence of alertness (as a function of the LC-NE system activation) on IOR, as elicited by the threat cues.

Recent views on emotional processing highlight the interactions between emotional and attentional systems (Okon-Singer, Hendler, Pessoa, & Shackman, 2015; Okon-Singer et al., 2013; Rohr et al., 2015). These views are based on evidence indicating that emotional information is prioritized and that it affects attentional functions, as well as evidence showing that attention and control mechanisms mediate reactions to aversive stimuli. Recent models further highlight the role of the thalamic pulvinar nucleus in the mutual influences of emotion and attention (Pessoa, 2013, 2017; Pessoa & Adolphs, 2010). The pulvinar nucleus has extensive connections to diverse cortical and sub-cortical regions, including to visual regions, fronto-parietal attention-related areas (Buchsbaum et al., 2006; Yuan et al., 2016) and the amygdala (Tamietto, Pullens, de Gelder, Weiskrantz, & Goebel, 2012). The pulvinar is connected to the superior colliculus, which mediates IOR (Sapir, Soroker, Berger, & Henik, 1999) and is a crucial node in the visual pathway. A large body of evidence shows that the pulvinar plays an important role in selective orienting of visual attention to relevant stimuli (Fischer & Whitney, 2012). Padmala, Lim, and Pessoa (2010) also suggested that the pulvinar is important in selective attention to emotional stimuli. Using an attentional blink task to modulate attention deployment to aversive and neutral stimuli, these researchers found that pulvinar activation was modulated by the aversive value of the stimulus only on correct trials and was additionally correlated with fluctuations in detection performance on these trials. These findings suggest that the pulvinar plays an active role in reactions to aversive information. This conclusion is in line with our suggestion in a previous study: Based on data from patients with brain injury, we suggested that the pulvinar may perform emotional tagging—a control process that determines whether a certain stimulus should be considered emotional and therefore receive prioritized processing (Arend, Henik, & Okon-Singer, 2015). Taken together, this evidence indicates that high arousal cues such as threat cues result in elevated NE secretion. This in turn leads to larger IOR mediated by activation in the superior colliculus. This is further associated with the tagging of information as threatening, which is mediated by pulvinar activation.

As noted, findings are mixed regarding the orienting of attention toward threat cues in spatial cuing tasks. Some studies showed reduced IOR following negative cues (Bertels et al., 2011; Pan et al., 2017; Pérez-Duenas et al., 2014; Shang et al., 2015), while others showed enhanced inhibition (Stormark & Hugdahl, 1996) or failed to find any differences between negative and neutral cues (Berdica et al., 2017; Hu et al., 2014; Stoyanova et al., 2007). How does our paradigm differ from previous research? We believe that the presentation of highly negative, colored pictures that are more negative than the stimuli employed in previous studies resulted in personal relevance and therefore enhanced processing. In support of this view, enhanced inhibition was also found by Stormark and Hugdahl (1996), who used the spatial cuing task with cues that were conditioned to a loud noise. These cues may have been more arousing and relevant to the participants than the cues used in other studies. Indeed, evidence indicates that personal relevance and task relevance modulate the orienting of attention to emotional distractors (Lichtenstein-Vidne, Henik, & Safadi, 2007, 2012). In these studies, the authors presented distractors while participants were engaged in a simple discrimination task. The distractors contained both task-relevant (e.g., their location when the central task was location discrimination) and task-irrelevant (i.e., their direction or their emotional valence) dimensions. The results showed that only task-relevant aspects affected performance in the discrimination task among healthy participants, as demonstrated by a congruency effect only for the location of the distractors but not for their direction or valence. Furthermore, patients with anxiety disorders were influenced by both the location and the emotional valence of the distractors (Lichtenstein-Vidne et al., 2017; see also Okon-Singer et al., 2011, for similar findings using emotional modification of a perceptual load task in participants with phobia). In addition, policemen who were repeatedly exposed to traumatic events were not influenced by highly arousing threat cues (Levy-Gigi, Richter-Levin, Okon-Singer, Kéri, & Bonanno, 2016). These findings highlight the role of personal relevance in orienting attention to environmental cues. Note, however, that we did not directly examine the perceived personal relevance of the picture cues, nor did we directly manipulate it. Future studies should directly examine whether personal relevance modulates IOR magnitude and time course either by asking participants to rate the personal relevance of the presented pictures or by manipulating the vividness of the aversive cues.

In the current study, the participants were healthy young adults. Understanding the orienting of attention to threat cues among healthy individuals is important both for identifying the factors that affect healthy behavior and also as a reference for assessing abnormal patterns of orienting among individuals with psychopathologies. Although numerous studies have examined attention functions in psychopathology, the reports in the literature are mixed and the exact conditions affecting the orienting of attention are not clear. In the context of threat, biases in attention are thought to be a core symptom of anxiety, with a causal role in initiating and maintaining the disorder (see discussion in Okon-Singer, 2018). This view is based on findings for enhanced vigilance followed by delayed disengagement and increased avoidance from threat in sub-clinical and clinical anxiety (see discussion in Okon-Singer & Aue, 2017). For example, anxious individuals responded more slowly to targets that appeared at invalid locations after negative than after neutral spatial cues (Koster, De Raedt, Goeleven, Franck, & Crombez, 2005). Support for this view also comes from attention bias modification (ABM) training studies, which used the dot-probe task to train anxious participants to orient attention away from threat cues and resulted in reduced anxiety and fewer stress symptoms (see meta-analysis in Price et al., 2016). Yet this view has also recently come under debate. In a comprehensive review, Mogg, Waters, and Bradley (2017) questioned the evidence for changes in attention bias to threat following ABM training, noting that in many studies participants with anxiety did not show an attention bias prior to the training. They suggested that the training had an influence on general attention functions, not specifically on orientation bias (for discussion see also Koster & Bernstein, 2015). In view of this debate, we suggest a change in paradigm, from the view that an attention spotlight moves to the threat cue and then to other locations to the view that parallel processes of facilitation and inhibition are separately influenced by different factors. These factors, among them level of cue processing and task- and personal-relevance, may explain the orienting of attention to threat among healthy as well as anxious individuals.

It is important to note a few limitations to our study. First, the pictures we presented were highly arousing as well as highly negative, and therefore we cannot disentangle the influence of arousal from that of their threat value. From an ecological point of view, threat cues involve both negative valence and arousal. Future studies should use highly arousing positive cues such as erotic pictures to examine whether the findings are due to arousal or to negative valence. In addition, since we did not directly manipulate cue processing, we cannot rule out possible confounding factors. Future studies should add a manipulation of cue processing in addition to valence, for example, by manipulating perceptual features that enable/prevent enhanced processing or by manipulating task difficulty.

In conclusion, in line with recent evidence indicating that enhanced processing of spatial cues leads to enhanced IOR, the current findings demonstrate a similar mechanism of increased IOR following threat cues compared to neutral cues. We consider IOR to be a mechanism that facilitates visual search by inhibiting reflexive orienting and favoring strategic/volitional processes. Negative spatial information is known to attract attention reflexively due to its evolutionary importance. Therefore, an enhanced inhibitory mechanism may be initiated in order to allow the individual to scan the environment effectively for other possible threats using voluntary attentional mechanisms.

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