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OBSERVATION

Knowledge of Collision Modulates Defensive Multisensory Responses to Looming Insects in Arachnophobes

Milou K. Huijsmans[1], Alyanne M. de Haan[2], Barbara C. N. Müller[1], H. Chris Dijkerman[2], and Hein T. van Schie[1]

[1] Behavioural Science Institute, Radboud University
[2] Department of Experimental Psychology, Helmholtz Institute, Utrecht University

We investigated the role of contextual knowledge in defensive responses to visual stimuli (spiders and butterflies) looming toward the hand. Human participants responded to tactile stimuli delivered to the same hand at 6 possible locations during an insect's approach. Tactile reaction times were faster when looming stimuli were closer to the hand, especially for spiders, and faster when insects loomed on a collision path than on a near-miss path. This latter finding suggests that human reactions to looming stimuli are not merely automatic reflexes but that contextual knowledge about the trajectory of looming objects is included in predicting their impact.

Public Significance Statement
We present evidence for the idea that the defensive system that protects us from harmful collisions with looming agents or objects uses knowledge about the trajectories of objects to modulate its response.

Keywords: defensive behavior, looming, spider, threat, peripersonal space

Supplemental materials: https://doi.org/10.1037/xhp0000974.supp

Protecting the integrity of the body is essential to ensure survival and reproduction. Evolution has produced a variety of defense mechanisms in animals to eliminate and avoid invisible pathogens, such as the immune system (Delves & Roitt, 2000), thermal regulation (Evans et al., 2015), and disgust (Curtis, 2011; Kupfer & Fessler, 2018). Furthermore, separate defense systems have evolved to detect and respond effectively to potential predators, such as hypersensitive agency detection (Maij et al., 2019) and fight, flight, and freeze reactions to threatening stimuli (Misslin, 2003). One specific mechanism that is considered to be crucial for survival is the ability to detect and respond to looming stimuli that are directed at one's body. Research in humans has suggested that defensive actions to looming stimuli are largely involuntary and mainly occur outside of the control of top–down voluntary mechanisms (Makin, Holmes, et al., 2009; van der Stoep et al., 2016). For instance, developmental studies have found that infants of only a few days old to several weeks of age respond defensively to looming optical shadows as well as real objects on a collision course, by tilting their head backward and raising their arms in front of their face in a protective gesture (Ball & Tronick, 1971), suggesting an inborn reflex. Furthermore, Makin, Holmes, et al. (2009) found activation in the motor system to be modulated already after 70 ms following the presentation of an unexpected looming object, which would leave little room for deliberation and top-down modulation of responses. In contrast, literature on animal behavior indicates that defensive behaviors are by no means

Milou K. Huijsmans https://orcid.org/0000-0003-3304-968X
Alyanne M. de Haan https://orcid.org/0000-0003-0896-0906
Hein T. van Schie https://orcid.org/0000-0002-1149-5198

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All data, stimuli and analysis scripts belonging to this research are available through the APA repository in the Open Science Framework via the following link: https://osf.io/myffu/?view_only=784046289d3746cfb80a3bf84fd16638.

Hein T. van Schie served as lead for conceptualization, investigation, supervision and writing – review and editing. Milou K. Huijsmans served as lead for data curation, formal analysis, investigation, methodology, project administration, software, visualization and writing – original draft. Alyanne M. de Haan served in a supporting role for writing – review and editing. Barbara C. N. Müller served in a supporting role for writing – review and editing. H. Chris Dijkerman served in a supporting role for writing – review and editing.

Correspondence concerning this article should be addressed to Hein T. van Schie, Behavioural Science Institute, Radboud University, Thomas van Aquinostraat 4, 6525 GD Nijmegen, the Netherlands. Email: hein.vanschie@ru.nl

stereotypical (McFadyen et al., 2020; Peek & Card, 2016) and that they may include contextual information in their decision making (Evans et al., 2019). For example, mice may choose from a selection of defensive behaviors such as freezing or fleeing depending on their distance from refuge (De Franceschi et al., 2016; Yilmaz & Meister, 2013), and fruit flies and goldfish perform preflight postural adjustments to determine the direction of their subsequent escape (Card & Dickinson, 2008; Foreman & Eaton, 1993). The present study sought to resolve this apparent contradiction between the animal and human literature by investigating the hypothesis that human responses to looming stimuli can also be modulated by top-down contextual information, similar to the findings as reported in the animal literature.

Method

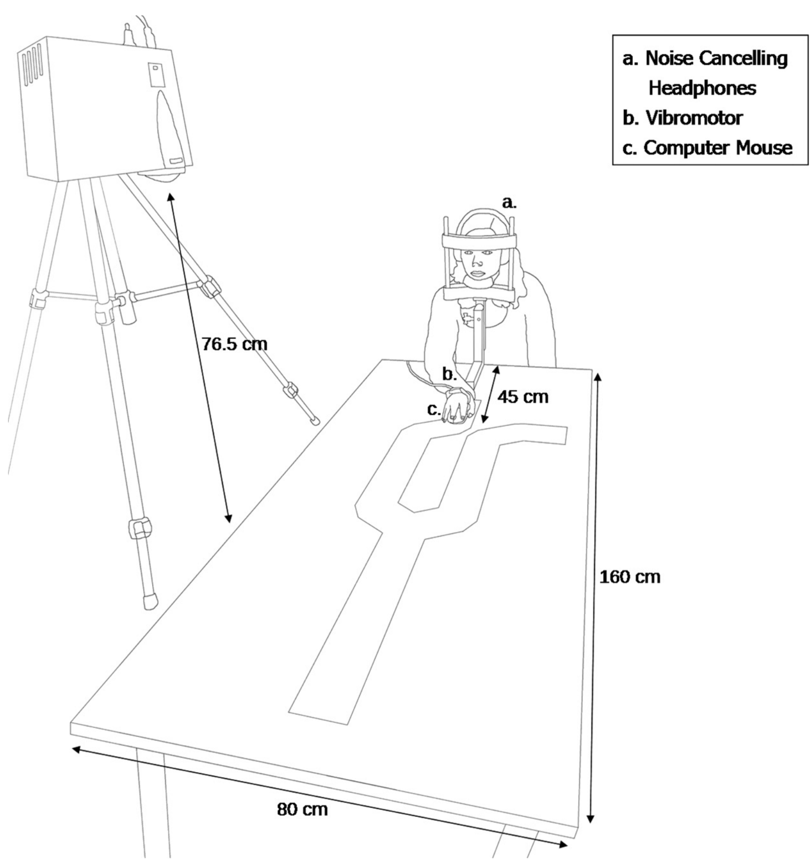
Experimental Design and Setup

To investigate the hypothesis that human responses to looming stimuli may be modulated by contextual information, we adapted the looming-insect paradigm by de Haan et al. (2016) and presented participants with two paths on which computer-animated insects, a spider or a butterfly, could travel toward the participant's hand (see Figure 1 and Figure 2), using a projector adjacent to the table (see videos in online supplemental materials). Insects traveling along one path would always end up at the participant's hand (the collision path), whereas insects traveling along the other path would always miss the hand by a few centimeters (the near-miss path). Similar to previous psychophysical experiments in this domain of study (Canzoneri et al., 2012; Cléry et al., 2015; de Haan et al., 2016; Kandula et al., 2015), tactile stimuli could be presented at various times during the approach of the looming object, and participants were instructed to press a mouse button as soon as they felt a tactile stimulus on the back of their hand. We used a procedure to make sure that the location at which a tactile stimulus could be presented was completely unpredictable to participants so that anticipation effects in reaction times (de Haan et al., 2016) could be prevented. Detailed information on technical details of the setup and this procedure can be found in the online supplemental materials. In line with the outcomes of the experiment by de Haan et al. (2016) we expected tactile reaction times to be faster (a) when looming stimuli were closer to the participant's hand, and (b) faster in response to approaching spiders than to approaching butterflies. Most importantly, following the contextual looming hypothesis, we expected tactile reaction times (c) to be faster for stimuli projected on the collision path than on the near-miss path.

Participants

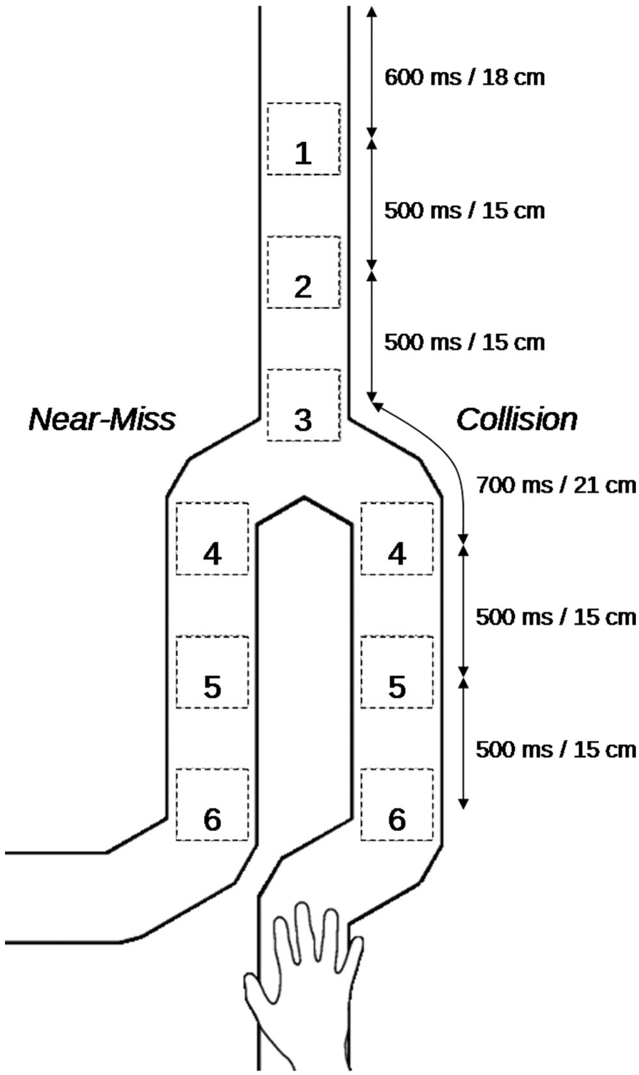
Participants were recruited via the university's research participation system and were offered a 10 Euro voucher or one course

Figure 1
Outline of the Experimental Setup



Note. See main text and online supplemental materials for further details.

Figure 2
Outline of the Two Pathways (Near-Miss and Collision) and the Six Tactile Stimulation Locations Indicated by Dashed Squares



Note. Dashed squares were not visible during the experiment.

credit as compensation. To assess eligibility to participate in the experiment, persons first had to complete online versions of the Fear of Spiders Questionnaire (FSQ) and Fear of Butterflies Questionnaire (FBQ). Only persons with at least moderate fear for spiders (FSQ $>$ 15) but not for butterflies (FSQ $<$ 15; Cochrane et al., 2008) were invited to participate in the experiment. Participants who completed the experiment had a mean FSQ score of 71.12 (SD = 13.86) and a mean FBQ score of 3.53 (SD = 3.81). A total of 19 participants were tested (see online supplemental materials for power analysis), two of which had to be excluded from analyses due to, respectively, an absence of mouse button-press responses and an unusually high number of RTs with a value of zero. All remaining participants were right-handed students between 18 and 30 years old (M = 23.06, SD = 3.38; 14 female).

Data Preparation and Statistical Analysis

Invalid responses and outliers were removed from the data, and the distribution of reaction times was normalized with a box-cox transformation; see online supplemental materials for details.

Because of the asymmetrical experimental setup of the study with a split in paths after location L3, data analysis was structured in two parts. The first analysis was directed at replicating the effects as described in the previous study by de Haan et al. (2016), more specifically the effect of location (L1 to L6), the effect of insect (spider, butterfly) as well as their interaction. To this end, the data collected at the collision and near-miss paths were pooled per location (L4, L5, and L6). The second analysis was directed at testing the influence of the two paths and selectively focused on locations L4, L5, and L6. Factors included in the analysis were path (collision, near-miss), location (L4, L5, L6), and insect (spider, butterfly).

As preregistered (https://osf.io/ngcrh/), two repeated measures ANOVAs were performed on the transformed mean RTs in R (R Core Team, 2017). Post hoc pairwise comparisons were performed with Bonferroni adjustments to the p values. To strengthen the reliability of the findings we also analyzed the data using linear mixed models (LMMs) in R; see online supplemental materials for technical details about the analyses and the results of the LMM.

All data, stimuli, and analysis scripts of this study are available in the Open Science Framework (Huijsmans et al., 2021).

Results

Evaluations of the stimuli indicated that participants rated the spider as significantly more threatening, frightening, intentional, and agentic than the butterfly, while both were evaluated as equally realistic; see online supplemental materials for statistics and mean ratings.

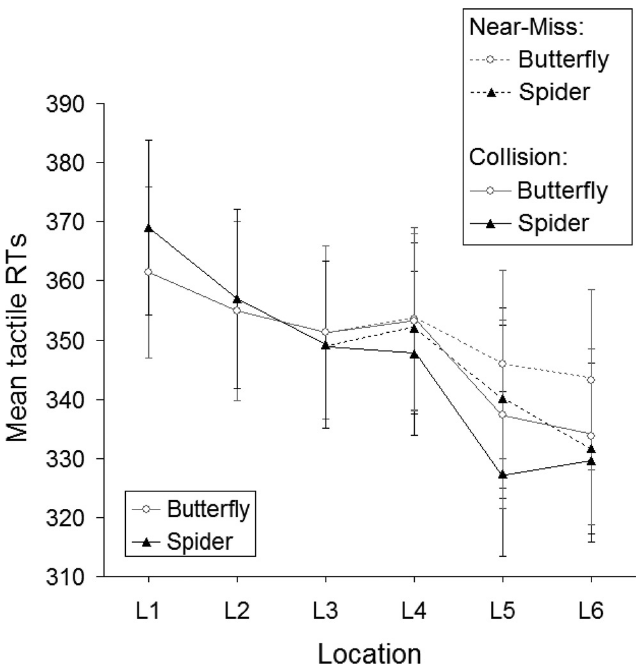
Effect of Insect and Location (L1 to L6)

The repeated measures ANOVA with within-subjects factors Insect (butterfly vs. spider) and Location (L1 to L6) revealed a significant main effect of Location on mean RTs, $F(5, 80) = 16.62$, $p < .001$, $\eta^2 = .05$, reflecting that insects elicited on average significantly faster RTs at locations closer to the hand. Although no significant main effect of Insect on mean RTs was found, $F(1, 16) = 3.34$, $p = .09$, we did find a significant interaction effect of Insect × Location on mean RTs, $F(5, 80) = 3.40$, $p = .008$, $\eta^2 = .004$, reflecting faster RTs for spiders than butterflies at locations L5 and L6; see Figure 3. Post hoc pairwise comparisons are reported in the online supplemental materials as are the results of the LMM analyses which generated the same pattern of significance as the ANOVA.

Effect of Insect, Location, and Path (L4 to L6)

The repeated measures ANOVA with within-subjects factors Insect (butterfly vs. spider), Path (collision vs. near-miss), and Location (L4 to L6) revealed a significant main effect of Location on mean RTs, $F(2, 32) = 10.00$, $p < .001$, $\eta^2 = .02$, indicating that, on average, RTs became faster when insects moved closer toward the body. Furthermore, a significant main effect of Insect on mean RTs was found, $F(1, 16) = 8.13$, $p = .01$, $\eta^2 = .007$, showing that, on average, the spider elicited faster RTs than the butterfly on locations L4 to L6. Importantly, the analysis showed a significant main effect of Path on mean RTs, $F(1, 16) = 9.69$, $p = .007$, $\eta^2 =$

Figure 3
Untransformed Mean Tactile Reaction Times (ms) at Locations L1 to L6 for the Butterfly and the Spider on Near-Miss Paths and Collision Paths



.007, as well as a significant interaction effect between Path × Location, $F(2, 32) = 3.84$, $p = .03$, $\eta^2 = .002$, indicating that RTs were faster for stimuli on collision paths than stimuli on near-miss paths, specifically at the final two locations L5 and L6, but not at L4. No other interaction effects were significant (all p values $>$ .37). In confirmation of the ANOVA, the LMM indicated a main effect of Path, but the interaction between Path × Location was not significant; see online supplemental materials for post hoc pairwise comparisons and the results of the LMM.

Discussion

Results confirmed the hypothesis that humans include contextual knowledge about the trajectories of looming objects in their anticipation of the impact of stimuli on the body. Tactile reaction times were faster on trials in which participants anticipated the insect to collide with their hand, relative to trials in which participants knew that the insect would miss their hand. This finding argues against the idea that defensive responses to looming stimuli are fully reflexive and impervious to contextual information (King et al., 1992; van der Stoep et al., 2016). Instead, this finding indicates that predictions concerning the impact of looming stimuli are not restricted to low level sensory features of looming stimuli such as velocity, direction, and proximity but that these predictions may also include contextual knowledge about the known trajectory of stimuli. The modulating effect of path also corroborates findings in ethology and the neurophysiology of looming responses in animals, which indicated that defensive behavior to looming stimuli may be modulated by contextual information and cognitive control processes supporting flexible behaviors to ensure survival of the organism (Evans et al., 2019; Peek & Card, 2016). The current study is one of the first to report a contextual influence on defensive responses to looming stimuli in humans (cf. McFadyen et al., 2020; see Sambo, Forster, et al., 2012 for comparable findings with the hand blink reflex) and thereby extends recent discoveries on the flexibility of looming responses in animals to humans.

Our finding that contextual knowledge may modulate responses to looming objects is furthermore consistent with anecdotal evidence from daily life and studies that have investigated human responses to looming stimuli in different settings. For instance, when people are waiting on the platform, they are typically not alarmed by the arriving train, which presents a strong looming stimulus. In this case the prior knowledge that the train will stay on the track may help to attenuate sensations of bodily impact. Furthermore, in sports such as baseball and cricket, looming objects present a target that is to be hit rather than avoided (Regan, 1997; Rushton & Wann, 1999). Likewise, other studies have found that looming information may be used for different purposes than defense such as visual control of breaking when driving a car (Lee, 1976) and the placing of footsteps when running on uneven terrain (Warren et al., 1986). Hence, looming stimuli may not always trigger defensive behaviors. Depending on the condition or task, such responses may be suppressed, modulated, or even reversed.

The effects of location and insect replicated the results by de Haan et al. (2016) who found that tactile RTs were faster when looming stimuli were closer to the participant's hand and that RTs were faster for trials with looming spiders than with looming butterflies. The former result confirms the longstanding literature on loomingness (Bufacchi & Iannetti, 2018; McFadyen et al., 2020), which states that the urgency of a defensive response is enhanced as a function of a looming stimulus' proximity. The latter result furthermore strengthens the idea that threat is a driving factor in the response to looming stimuli (cf. Basanovic et al., 2019; de Haan et al., 2016; Vagnoni et al., 2012). Note, however, that this latter result should be considered with some caution as low-level physical properties of spider and butterfly stimuli were not controlled for in the present study design.

Several additional limitations of the current study should be noted as well. First, following the approach by de Haan et al. (2016), we only admitted participants who were afraid of spiders and not of butterflies (19 out of 47 screened participants). Second, we used a convenience sample consisting of university students who were all right-handed and in majority female. As a consequence, we should be careful with generalizing our findings to the general population. Although our results are line with the hypothesis that shared phylogenetic mechanisms serve defensive behaviors in both animals and humans, further research is necessary to replicate our findings in a larger and more representative human sample.

In sum, the psychophysical evidence presented in the current study supports the hypothesis that humans can use contextual knowledge in anticipating the time and location of collision with looming stimuli. These findings extend recent discoveries in animal ethology and animal neurophysiology to humans and call for a closer integration between both literatures. Moreover, the results corroborate the neuroscientific consensus that phylogenetically ancient mechanisms underlie the capacity of a virtually all animals with sufficiently detailed vision a to protect themselves from looming objects (Peek & Card, 2016). In addition, the findings reported may hold relevance for different theoretical perspectives that are conceptually related to the detection and response to looming stimuli such as models of peripersonal space (Bufacchi & Iannetti, 2018), the framework of predictive processing (Friston, 2010), the defense cascade model (Lang et al., 1997), and models of interception (Brenner & Smeets, 2018); see online supplemental materials for more information about the relevance of our findings for these models. We hope that the present study will contribute to a further integration of these theoretical perspectives to advance our understanding of human defensive behavior.

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