

Short report

The effect of stimulus encounter rate on response decrement in jumping spiders

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ABSTRACT

The inability to maintain signal detection performance with time on task, or response decrement, has been widely studied. In animals with small brains, the ability to filter out repetitive, irrelevant stimuli may prevent the nervous system from being saturated with information. However, animals must be particular to which stimuli they attend and those to ignore, as mistakes may be costly. We explored the effect of inter-stimulus interval (ISI) between repeated presentations of a visual stimulus on the response decrement of the jumping spider *Trite planiceps*. Jumping spiders are active visual hunters, and moving visual stimuli trigger a readily observable optomotor response. We used either an ISI of 10 or 20 s between 160 stimulus presentations, predicting that a shorter ISI would result in a steeper decrement through cognitive overstimulation, according to the resource depletion theory. While a clear response decrement was seen for both conditions, the shorter ISI resulted in a more dramatic response decrement, aligning with the resource depletion theory posited in the human-based literature.

1. Introduction

How do animal brains classify what stimuli to attend and which to ignore? What is the effect of stimulus repetition, and encounter rate, on these decisions? These questions have been well-studied using behavioural, psychophysical (Mackworth, 1968; Rose and Rankin, 2001) and physiological (Byrne, 1982; Araki and Nagayama, 2005; Glanzman, 2009) measures in both humans and in many invertebrates, although largely neglected in spiders.

There is considerable human-based literature on how behavioural responses decrease over time when faced with repetitive stimuli. This response or vigilance decrement literature posits two theories, evidence for which has been found for both. The underload theory predicts a faster decrement in less challenging tasks, positing that these provide too little cognitive load, so the attentional system reduces effort through understimulation (Pattyn et al., 2008). In contrast, the resource depletion theory (Helton and Warm, 2008) expects a faster decrement in tasks that are cognitively demanding (overstimulating), such that challenging tasks ‘burn up’ replenishable necessary attentional resources, or lead to reallocation of those resources in order to facilitate recovery, analogous to a running animal slowing down to facilitate skeletal muscle recovery (Helton et al., 2002).

As attested by the widespread use of animal model systems, there is merit in using animals with less complex brains to examine processes affecting humans. To this end, we examined the response decrement in the jumping spider (Salticidae) *Trite planiceps*. As visual predators, salticids have a forward-facing pair of ‘anterior-medial’ eyes specialised for high acuity vision within a narrow (< 5°) field of view. Additionally, salticids have three pairs of motion-sensitive secondary eyes, the ‘posterior-lateral’, ‘posterior-medial’, and ‘anterior-lateral’ (AL) pairs, with wide fields of view collectively encompassing ca. 360° (Land, 1985). When hunting, movement detected by the secondary eyes over their wide field of view may elicit an optomotor response whereby the spider pivots to ‘face’ the source of movement with the anterior-medial eyes for closer inspection. This unambiguous response is an excellent cue for determining salticid perception of an ‘interesting’ visual stimulus and consequently provides insights on their attention-based decisions.

We investigated the effect of inter-stimulus interval (ISI) on the response decrement in *Trite planiceps*. Based on previous work on invertebrates (Rose and Rankin, 2001; Araki and Nagayama, 2005), we expected a steeper response decrement which would then plateau at a lower level when stimuli were presented at higher encounter rates.

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2. Methods

Detailed methods, including spider housing and maintenance, were as previously described (Melrose et al., 2018). Briefly, wild-caught adult and subadult female spiders were laboratory acclimated for > 7 days before testing, which was performed between 0700–1300 hours in a temperature-controlled room (25 °C). Salticids were tested once and all tests were conducted one day after feeding.

For testing, spiders were placed equidistant from two identical 17" stimulus-presentation monitors (see supplementary materials) placed 120° from each other. Spiders were suspended within the apparatus using a drop of beeswax to the top of the cephalothorax, which was attached to a TPC® micro-applicator, itself attached to the testing apparatus by a crocodile clip (see Humphrey et al., 2018). Test spiders were given a 17 mm crosshair-marked polystyrene ball to hold, as in previous experiments (Zurek et al., 2010; Melrose et al., 2018). The ball was cleaned with 70% ethanol between tests. Once in place, the spider was given 20 min to recover from handling stress before testing began.

The stimulus was a 13.5 mm black circle presented on a grey background. The 5 s stimulus crossed on the horizon of the spider's field of view and moved from posterior to anterior and was visible solely to the AL eyes (see supplementary materials). The stimulus subtended 1.3° from the point of view of the test subject and the 160 repetitions (trials) alternated between monitors.

Two groups of five salticids were tested: group 1 had an ISI of 20 s; group 2 had an ISI of 10 s. Stimulus presentation (ISI rate) was controlled using a custom-written program using C#. NET on Microsoft Visual Studios 2010. All tests were filmed from above for later scoring.

Stimulus responses were scored as binary: the salticid's orienting response causes the polystyrene ball that the spider is holding to rapidly swivel in the opposite direction (scored as 1); and failure to perform an optomotor response was scored as 0. For analysis in R (R Core Team, 2014), we used generalised linear mixed models with trial as a random effect and ISI as a fixed effect. The family was set as binomial, and the link function as Logit and set to a Laplace approximation (Waller et al., 2013).

3. Results

There was a significant decrease (estimate, z and P are in parenthesis for all results) in responses over time for both the 10 s (-1.0701, -6.98, $P < 0.0001$) and the 20 s ISI experiments (-0.720, 5.766, $P < 0.0001$). Additionally, there was a significantly stronger decrement (and a lower overall plateau level) in the 10 s experiments compared with the 20 s experiments (0.241, 2.026, $P = 0.043$). For both experiments (see Fig. S2 for pooled raw data and Figs. S3-12 for raw data on individual spiders), the decrease was rapid during the first 15 trials, and was then followed by a slower decline which resulted in an

oscillating low response level over the remainder of the trials (Fig. 1). For the 10 s ISI, the intercept was 0.83 and the decay slope, with x defined as trial number, was $Y = \exp(-0.2979(x + 1.662385)) + 0.224$, while the more gradual 20 s ISI slope was $Y = \exp(-0.1804(x + 4.2824)) + 0.224$ and had an intercept of 0.69.

4. Discussion

There is a vast literature on human 'vigilance decrement' due to its effects for time-on-task for repetitive - yet very important - jobs, such as air-traffic control operators. Under different names (usually habituation), this widespread phenomenon has been studied in many invertebrates, beginning with Kandel's pioneering work on the gill withdrawal reflex in *Aplysia* (Pinsker et al., 1970; Glanzman, 2009). The effect of ISI, in which faster stimulus encounter rate leads to a more pronounced loss of response, has been investigated in several invertebrates (e.g., crayfish, Araki and Nagayama, 2005, *Aplysia*, Byrne, 1982, nematodes, Rose and Rankin, 2001), but this is the first study to examine its effect in spiders. As with the studies mentioned above, a shorter ISI between stimuli led to a significantly steeper decrement in *T. planiceps*, which led to a lower response level throughout the remaining trials, compared with the longer ISI. These results closely mirror findings in nematodes (Rose and Rankin, 2001).

Our results were based on a limited sample size. A larger sample size would reduce variability, yet the effects were still evident. We suggest that these findings align with the resource depletion theory in that the rapid encounter rate of the stimulus was overstimulating to the spider's limited neural capacity, giving it little chance to recover between presentations. While both classical sensory habituation and resource depletion theory, but not underload theory, would predict a steeper decrement with a shorter ISI, we propose that the decrement is unlikely to be entirely due to sensory habituation. Using a simple dot stimulus like the one used here, we previously demonstrated that a dishabituating stimulus presented in a different sensory modality does not affect the response decrement (i.e., the decrement continues as in control situations without dishabituation; Melrose et al., 2018). This is not in line with a decrement due to sensory habituation, where dishabituation results in detection recovery (Mackworth, 1968). Additionally, for both hungry and sated spiders, changing task difficulty by varying the signal:noise ratio affects the rate of decrement, with stimulus contrast being the key variable affecting response decrement in *T. planiceps* (Humphrey et al., 2018). The sum of these results aligns better with the resource depletion theory than with the underload theory.

An alternative hypothesis is that physical fatigue might have led to the steeper decrement in the shorter ISI condition. We believe this unlikely, as we have previously found no change in walking behaviour during testing, but a similar decrement in the optomotor response to the repeated stimulus (Humphrey et al., 2018), and, after 160 trials, spiders

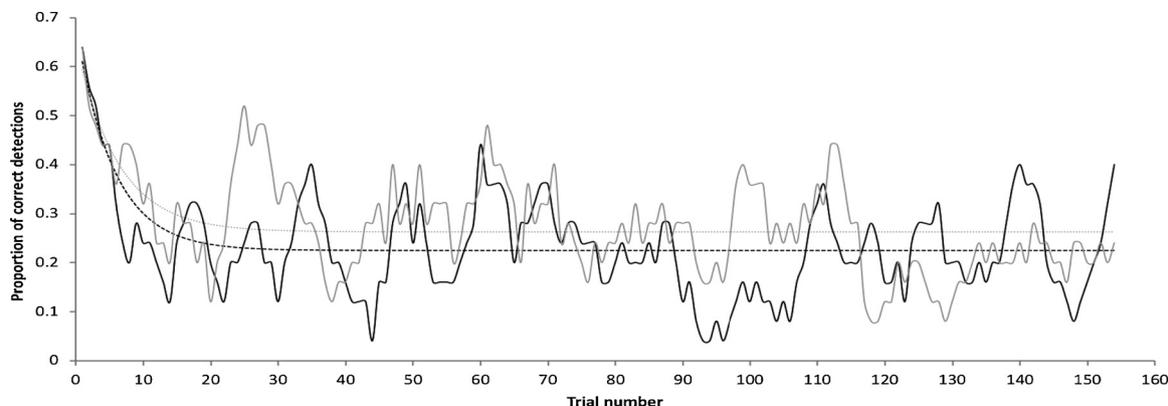


Fig. 1. Smoothed data (solid lines) of the responses of *Trite planiceps* spiders to a visual stimulus with 10 s (black) and 20 s (grey) inter-stimulus intervals. Data were smoothed using a moving average of 5 trials and were fitted with a non-linear exponential function (dotted lines).

here responded at similar levels to tests with only 80 trials (Melrose et al., 2018), yet we would have expected the decrement to continue to decline over time in these longer tests. Additionally, salticids did not show a gradual decline, as is typical of fatigue (Cooper et al., 1988); instead, as seen in *Aplysia*'s gill-withdrawal reflex (Pinsker et al., 1970), spiders quickly decreased their response rate and then maintained an oscillating low baseline throughout the remaining trials. The oscillations seen in our dataset are similar to those seen in other animals (e.g., nematodes, Rose and Rankin, 2001), and may reflect some kind of period during which depleted resources are replenished; this is an area of future enquiry. Overall, our results suggest that *T. planiceps* responds to repeated presentation of a visual stimulus with a rapid decrement which is affected by stimulus encounter rate, with shorter ISIs leading to a more pronounced loss of response.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.beproc.2018.12.020>.

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