

March 2019

Visual Attention in Jumping Spiders

Margaret Bruce
University of Massachusetts Amherst

Follow this and additional works at: https://scholarworks.umass.edu/masters_theses_2



Part of the [Behavior and Ethology Commons](#), [Biology Commons](#), [Entomology Commons](#), and the [Evolution Commons](#)

Recommended Citation

Bruce, Margaret, "Visual Attention in Jumping Spiders" (2019). *Masters Theses*. 736.
<https://doi.org/10.7275/p2fj-y737> https://scholarworks.umass.edu/masters_theses_2/736

This Open Access Thesis is brought to you for free and open access by the Dissertations and Theses at ScholarWorks@UMass Amherst. It has been accepted for inclusion in Masters Theses by an authorized administrator of ScholarWorks@UMass Amherst. For more information, please contact scholarworks@library.umass.edu.

2019

Visual Attention in Jumping Spiders

Margaret Bruce

Follow this and additional works at: https://scholarworks.umass.edu/masters_theses_2

 Part of the [Behavior and Ethology Commons](#), [Biology Commons](#), [Entomology Commons](#), and the [Evolution Commons](#)

Visual Attention in Jumping Spiders

A Thesis Presented

by

MARGARET A. BRUCE

Submitted to the Graduate School of the
University of Massachusetts Amherst in partial fulfillment
of the requirements for the degree of

MASTER OF SCIENCE

February 2019

Organismic & Evolutionary Biology Graduate Program

Visual Attention in Jumping Spiders

A Thesis Presented

by

MARGARET A. BRUCE

Approved as to style and content by:

Elizabeth M. Jakob, Chair

Paige S. Warren, Member

Jeffrey Podos, Member

Paige S. Warren, Program Leader
Organismic & Evolutionary Biology

ACKNOWLEDGEMENTS

I would like to thank my advisor, Elizabeth M. Jakob, for her years of invaluable support and guidance with my research as well as my long-term career goals. I would also like to thank the other members of my committee, Paige Warren and Jeff Podos, for their support and guidance, and for being flexible with my changing schedule. Thanks are also due to Skye Long, who taught me to use the eyetracker and was always available to answer my questions, offer advice, and troubleshoot my stimulus codes.

I also want to thank Daniel Daye for the countless hours he put into this research, and his support and friendship through the entire analysis and writing process.

Finally, a special thank you to all those, especially Jacob Bear, Elsa Cousins and Carolyn Anderson, whose support and friendship helped me to focus on this project and encouraged me to keep going even when things got complicated.

ABSTRACT

VISUAL ATTENTION IN JUMPING SPIDERS

FEBRUARY 2019

MARGARET A. BRUCE, B.A., BOSTON UNIVERSITY

Directed by: Dr. Elizabeth M. Jakob

The different ways that animals extract and analyze visual information from their environment is of interest to sensory ecologists. Jumping spiders, well-known for visually guided mating and hunting behavior, are an interesting model for the study of visual attention because they quickly and efficiently integrate information from eight eyes with a small brain. Stimuli in front of the spider are examined by two functionally and morphologically distinct pairs of forward-facing eyes. The principal eyes discern fine details and have small retinas and thus a small visual field. However, their position at the back of moveable tubes within the cephalothorax expands this visual field. The anterolateral eyes, one of the three pairs of secondary eyes, have lower spatial acuity and a larger visual field that overlaps with that of the principal eyes. They act as motion detectors, directing the principal eyes to objects appearing in their visual field. In Chapter 1, using a salticid-specific eyetracker, I explore how characteristics of a stimulus influence whether the secondary eyes redirect the gaze of the principal eyes from a principal stimulus to a new stimulus appearing in the visual field. I found that spiders suppressed redirection of the principal eyes when engaged by a salient stimulus, and redirected to moving peripheral stimuli more frequently than to stationary peripheral stimuli.

The principal eyes are also known to engage in a complex behavior called “scanning,” involving both dorsoventral and rotational movement. One hypothesis regarding scanning’s function is that it helps spiders identify important lines and angles in stimuli. However, scanning routines are not well understood. In Chapter 2, I measured scanning behaviors when spiders were watching quickly moving versus still or slowly moving images. I found that spiders spent more time overall looking at still or slowly moving images, and that stimulus speed does not appear to affect rotational movement of the retinas. Overall, I conclude that motion in an appearing stimulus elicits the attention of the principal eyes, but it remains unclear how and whether scanning functions in the extraction of detail from moving stimuli.

TABLE OF CONTENTS

	Page
ACKNOWLEDGEMENTS	iii
ABSTRACT	iv
LIST OF FIGURES	vii
CHAPTER	
I. SHIFTS OF VISUAL ATTENTION IN JUMPING SPIDERS	1
A. Abstract	1
B. Introduction	1
C. Materials and Methods	4
D. Results	6
E. Discussion	8
II. RETINAL MOVEMENT CHANGE WITH SPEED OF VISUAL STIMULI	11
A. Abstract	11
B. Introduction	11
C. Materials and Methods	14
D. Results	16
E. Discussion	19
BIBLIOGRAPHY	22

LIST OF FIGURES

Figure	Page
1.1. Response to peripheral stimulus based on type of primary stimulus.....	7
1.2. Response to peripheral stimulus based on type of peripheral stimulus.....	8
2.1. The effect of stimulus speed on the overlap of the retinas with the stimulus.....	17
2.3. The effect of stimulus speed on the average angle change of both retinas.....	18
2.4. The effect of stimulus speed on angular directional change of retinas	19

CHAPTER I

SHIFTS OF VISUAL ATTENTION IN JUMPING SPIDERS

A. Abstract

Jumping spiders have a visual system consisting of functionally and morphologically distinct pairs of eyes that overlap in their field of view. While the principal eyes detect fine detail and have a small field of view, the anterior lateral eyes have a wide field of view with coarser vision, and act as motion detectors. Here, a salticid-specific eyetracker was used to monitor retinal movements. Spiders viewed a video of a pair of visual stimuli: a primary target stimulus and a peripheral stimulus, which appeared after the primary stimulus. This tested the malleability of the relationship between the principal and secondary eyes, and whether the redirection of attention to a new stimulus can be suppressed depending on the salience of the stimulus. Spiders' attention shifted from a non-salient stimulus more frequently than it did from a putatively salient stimulus, and moving stimuli more frequently caused a redirection of attention. These findings suggest that the relationship between the principal and secondary eyes is plastic and attentional shifts depend on the nature of both the primary and peripheral stimuli.

B. Introduction

Attention is the process of focusing on a selected aspect of a complex, multifaceted environment. In humans and other vertebrates, visual attention is often assessed by measuring gaze direction via eye or head movements (Corrigan et al. 2017 , Land and Hayhoe 2001, Tatler et al. 2010, Yorzinski et al. 2013, Yorzinski et al. 2015, Yorzinski et al. 2017). However, although selective visual attention has been

demonstrated in invertebrates (Giurfa and Menzel 1997, Morawetz and Spaethe 2012, Spaethe et al. 2006, van Swinderen and Greenspan 2003, Wiederman and O'Carroll 2013, Humphrey et al. 2018), precise gaze direction can be very difficult to monitor in these animals (Land 1995). Here, we use a custom-built modified ophthalmoscope (Jakob et al. 2018, Canavesi et al. 2011) to record the gaze direction of jumping spiders, *Phidippus audax*, and test how gaze direction is influenced by the presence of appearing peripheral stimuli.

Jumping spiders (Family Salticidae) are well known for their visually guided behaviors, especially courtship and predation (Harland & Jackson 2012). These spiders possess a visual system distinct from both vertebrates and insects that allows for unique solutions to the challenges of visual attention. The visual system consists of a set of moveable principal eyes which possess the best spatial acuity known for a terrestrial invertebrate (Warrant & McIntyre 1993) which overlap in their field of view with the stationary anterior lateral secondary eyes (reviewed in Land and Nilsson 2012). The ALEs are less spatially acute than the principal eyes but have a larger field of view, and serve to direct the movement of the principal eyes to moving objects and objects that suddenly appear, much like motion detectors (Jakob et al. 2018). Thus, a spider can monitor a broad field of view but direct its high-acuity eyes quickly to examine objects of interest. Once the principal eyes are directed to an object, spiders exhibit a unique behavior called scanning, in which the retinas are moved repeatedly over the stimulus field while being rotated (Land 1969a).

The question arises as to whether a spider examining an object with its principal eyes should always redirect its principal eyes to a new stimulus when it is detected by the

ALEs. In some cases, it may be evolutionarily beneficial to suppress distraction from a target stimulus. For example, dragonflies can track the movements of a single individual in a swarm of flies without getting distracted by the movements of other flies (Wiederman and O'Carroll 2013). In contrast, when presented with distractors in a visual search task, honeybees frequently make incorrect decisions when choosing a target (Spaethe et al. 2006, Morawetz and Spaethe 2012). In still other cases, failing to attend to peripheral stimuli may be costly: animals face a trade-off between focusing on a single task and remaining vigilant. Blue jays attending to a difficult foraging task are hindered in their ability to detect a target in the peripheral field, which could be a predator (Dukas and Kamil 2000). Similarly, a pilot experiment suggested that salticids may suppress a redirection of their principal eyes to a new, potentially relevant stimulus appearing in the field of view of their ALES when they are visually “locked on” to prey. *Freya pachomius* jumping spiders that were watching a video of a moving cricket were captured more quickly in a vial approaching from the side of the arena than were spiders looking at a blank screen. Furthermore, a recent study showed that vigilance in jumping spiders decreases with the complexity of a visual stimulus (Humphrey et al. 2018).

Here, we used a spider eyetracker to test the malleability of the relationship between the principal and secondary eyes, and whether a redirection of attention to an appearing peripheral stimulus can be suppressed. We showed spiders videos of pairs of stimuli: a primary target stimulus and a peripheral stimulus, which appeared after the primary stimulus and while the spiders were looking at the primary stimulus. First, we varied the qualities of the primary stimulus, and in a second experiment we varied qualities of the peripheral stimulus.

C. Materials and Methods

We tested 31 adult female *Phidippus audax* jumping spiders, captured using sweep nets and vials from fields and metal structures in Hampshire County, MA, USA. Spiders were housed in a lab kept at 25° C and with a 16L:8D light cycle. They were kept in individual plastic boxes (18 x 13 x 10 cm), and provided a stick, a hollow black tube, and plastic foliage for habitat enrichment (Carducci and Jakob 2000). Spiders were fed crickets (*Acheta domesticus*) once weekly and provided with water *ad libitum*.

We used a customized salticid-specific eyetracker (Jakob et al. 2018, Canavesi et al. 2011) to map the changing position of spiders' principal eye retinas as they viewed stimuli. The eyetracker is a modified ophthalmoscope that uses infrared light (Thorlabs IR 850 nm Mounted High-Power LED 1000 mA with T28 Cube LED Driver, directed with an Edmund's dual branch light guide #54202 equipped with 29 Thorlabs OSL2 focusing lens) shined through the spider's carapace, and was inspired by the work of Land in 1969 (Land and Nilsson 2012, Land 1969a,b). The image of the retinas is overlaid and aligned with stimulus videos, resulting in data similar to those generated in human-eyetracker research (Jakob et al. 2018).

During a trial, individual spiders were tethered with a plastic microbrush (Easyin smile dental disposable 38 microapplicator brush) attached to the cephalothorax using a mixture of gum rosin (Acros Organics) and beeswax (Stackich) (Jakob et al. 2018). The waxed microbrush was then painted with blackboard paint (Americana Chalkboard Paint) to eliminate glare from the infrared light.

Once tethered and aligned in the eyetracker (see Jakob et al. 2018 for details), spiders were presented with a trial video. Using Processing (v 2.2), we created a program

that presented a primary stimulus at the center of a spider's visual field, which was ascertained prior to the experiment using a calibration program (jakob et al. 2018). Once spiders' retinas were clearly engaged with the primary stimulus, we presented the peripheral stimulus in an area of the screen only visible to the secondary eyes. In the first experiment, we used multiple primary stimuli but kept the peripheral stimulus constant. Primary stimuli included a black cricket silhouette (N = 16), a black oval (N = 16), or a treatment with no stimulus at all (N = 15). The peripheral stimulus was a black oval in every treatment. One trial consisted of one spider receiving each treatment in random order with a 3-minute break in between each presentation.

In the second experiment (N = 15), we tested whether the type of peripheral stimulus influenced a shift in gaze direction by the principal eyes. Spiders always began these trials by examining a cricket silhouette as the primary stimulus. Peripheral stimuli were presented in random order and included a cross, a cricket, a rapidly expanding ("looming") circle, and a rapidly shrinking ("receding") circle. Jumping spiders are known to ignore receding stimuli but respond to and back away from looming stimuli, a response mediated by the secondary eyes (Spano et al. 2012). Pilot data also suggests that spiders in the eyetracker spend some time scanning images of crosses, which bear some resemblance to cricket antennae and the upraised legs of spiders, but not as much time as they spend on cricket silhouettes.

For both experiments, I video-recorded trials and scored whether or not a spider shifted its gaze from the primary stimulus to the peripheral stimulus immediately upon its presentation.

D. Results

In the first experiment, spiders looked at the peripheral stimulus significantly more frequently when there was no primary stimulus or an oval stimulus than when the cricket primary stimulus was presented (Fig. 1.1, Pearson's Chi-squared, $\chi^2=17.73$, $df=2$, $P=0.0002$). In the second experiment, there was a trend in spiders' response to the four different peripheral stimuli (Pearson's Chi-squared, $\chi^2=7.33$, $df=3$, $P=0.0628$). When I combined moving stimuli (looming or shrinking) and stationary images (cross or cricket), spiders were significantly more likely shift their gaze to moving stimuli. (Fig. 1.2, Pearson's Chi-squared, $\chi^2=5.50$, $df=1$, $P=0.019$).

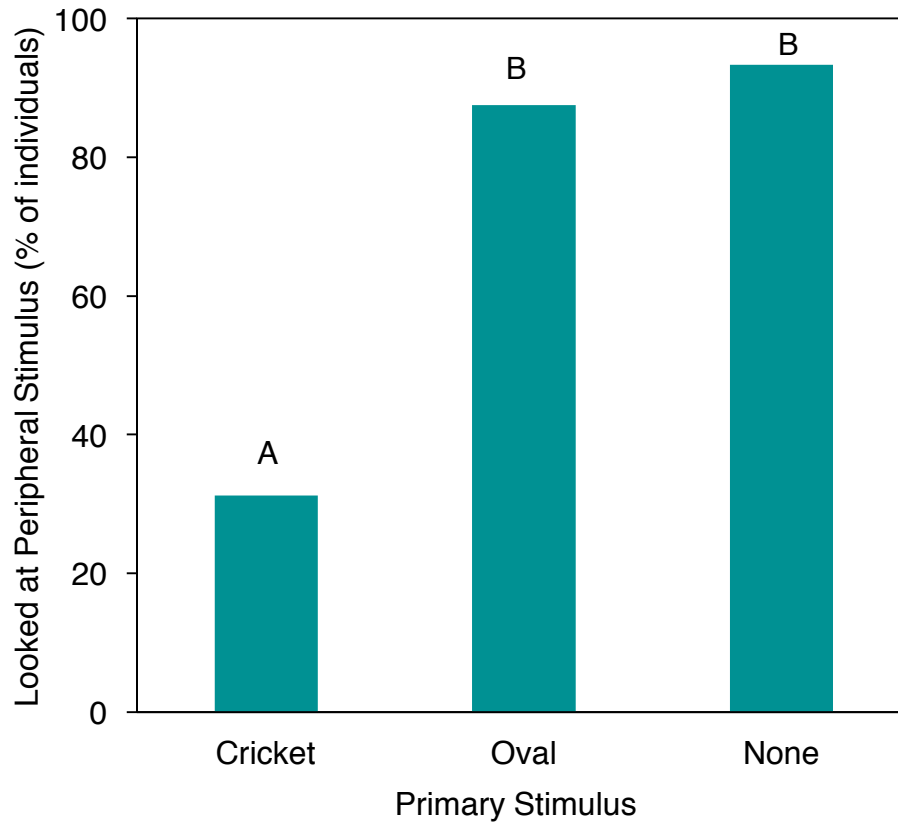


Figure 1.1. Response to peripheral stimulus based on type of primary stimulus. Spiders shifted their gaze to the peripheral stimulus significantly less often when the primary stimulus was a cricket.

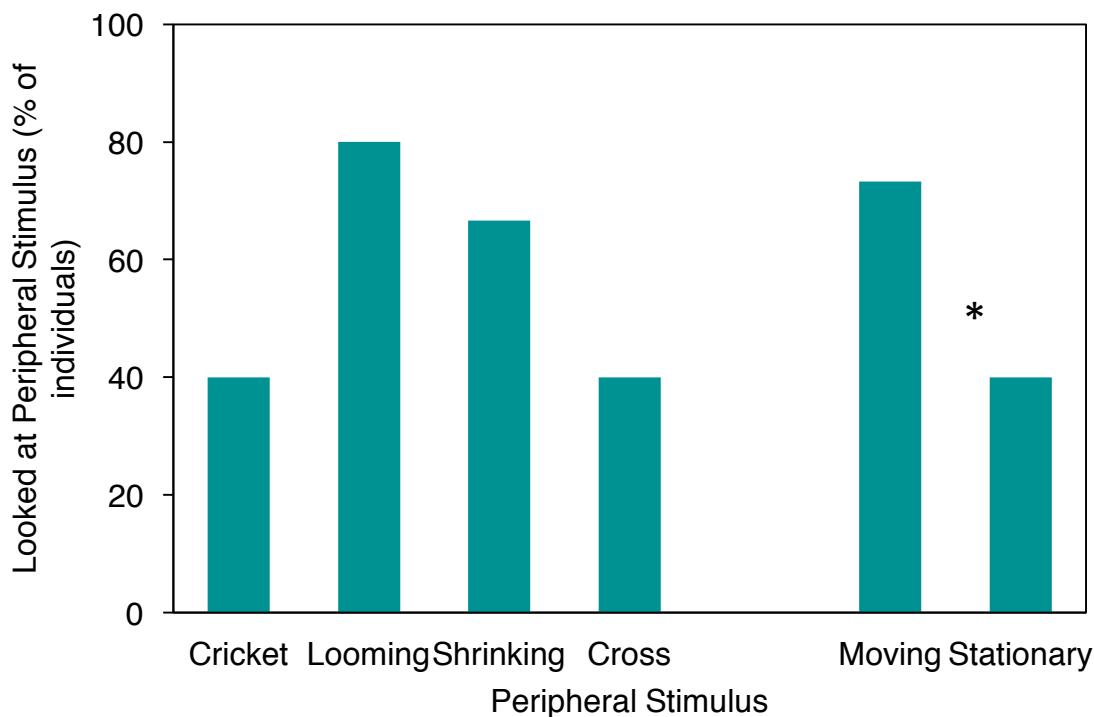


Figure 1.2. Response to peripheral stimulus based on type of peripheral stimulus. There was a tendency for responses to all four stimuli ($P < 0.07$); when moving (looming and shrinking) and stationary (cricket and cross) were combined, differences were significant.

E. Discussion

Spiders' propensity to shift the gaze direction of their principal eyes to a new stimulus detected by the ALES depended on characteristics of both the primary (Experiment 1, Figure 1.1) and peripheral (Experiment 2, Figure 1.2) stimuli. These findings demonstrate that the redirection of attention of the principal eyes by the ALES is plastic.

These results are relevant to the important function of 'distractability' in a complex environment where an animal must forage and avoid predators simultaneously. Failure to notice an approaching predator while examining a prey item could be fatal.

Indeed, some evidence suggests that predators selectively attack prey that appear to be distracted by a foraging task (Krause and Godin 1996). A larger body of evidence supports the hypothesis that animals already attending to a stimulus are less likely to respond to approaching predators (Blumstein 1998, Brick 1998). For example, blue jays fail to detect peripheral targets while engaged in difficult foraging tasks (Dukas and Kamil 2000), and guppies exhibiting a nose-down foraging posture are less likely to flee from a predator model than those not engaged in foraging or exhibiting a different, horizontal foraging posture (Krause and Godin 1996). Humans, as well, pay less attention to peripheral moving stimuli when performing a difficult central task (Rees et al. 1997). This pattern is also found in jumping spiders: recent research shows that vigilance decreases as visual tasks increase in difficulty (Humphrey et al. 2018). The current experiment shows that while spiders' propensity to examine a distracting stimulus is diminished when they are examining a salient object, they appear able to "flip" their focus from the object if the distracting stimulus is in motion. Indeed, wasps, well-known predators of spiders (Finch 2005, Schlinger 1987), move quickly and may descend from above or approach laterally, much like a looming stimulus.

These results are also reflected in our current understanding of spider neurophysiology. In the central nervous systems of all spiders, input from the principal and secondary eyes is processed independently until being combined later in the neural pathway (Strausfeld et al. 1993, Strausfeld and Barth 1993, Barth 2001, Long 2016). There are two pre-protocerebral optic neuropils associated with each secondary eye (ON1 and ON2), and a single third optic neuropil, known as the mushroom body, shared by all secondary eyes (Barth 2001). Similarly, there are three visual neuropil regions associated

with the principal eyes: AMON1, AMON2, and the arcuate body, which is likely a visual center (Barth 2001). In jumping spiders, the arcuate body is connected to the secondary eyes as well as the principal eyes, and possibly acts as an integration center for information from these two sets of eyes. More support for this hypothesis comes from neurophysiological recordings made in jumping spiders, where spatiotemporal receptive fields were only recorded in or near the arcuate body when both sets of eyes were unoccluded (Menda et al. 2014). Jumping spiders appear to be the only spiders that exhibit communication between the secondary eyes and the arcuate body (Strausfeld 2012).

In the second experiment, spiders looked at both looming and receding peripheral stimuli with comparable frequencies. Previous work investigated spiders' physical response to looming stimuli, finding that they back away from them (Spano et al. 2012). However, Spano et al. also found that spiders showed no response to a receding stimulus. Taken together, these results indicate that the spiders in this experiment were able to detect the receding stimulus, but did not physically react to it, suggesting the involvement of higher-order processing in mediating the response to visual stimuli.

CHAPTER II

RETINAL MOVEMENT CHANGE WITH SPEED OF VISUAL STIMULI

A. Abstract

Jumping spiders (Family Salticidae) are well-known for their visually guided courtship and predatory behaviors. These behaviors are mediated by two functionally and morphologically distinct forward-facing pairs of eyes: the principal, or anterior median, eyes, which small field of view but are moveable; and the secondary, or anterior lateral eyes, which are stationary and have a larger field of view. The narrow, boomerang-shaped principal eye retinas exhibit a unique pattern of movement called scanning, in which they simultaneously move along the dorso-ventral or latero-medial planes and rotate around a central axis. Using a custom-built salticid-specific eyetracker, we observed that scanning behaviors can last up to several minutes. However, spiders in the wild must make split-second decisions about when to approach quickly moving prey items. Using the eyetracker, we tested whether *Phidippus audax* jumping spiders scan quickly moving stimuli as extensively as they appear to scan slowly moving stimuli. We found that spiders spend less time overall looking at quickly moving images compared to images moving more slowly, but found no evidence that stimulus speed has an effect on rotational motion. We suggest that evaluation of fast-moving stimuli may be mediated by the anterior lateral eyes, and recommend avenues for future investigation.

B. Introduction

Across the animal kingdom are many species whose retinas possess foveas, or areas of higher ganglion cell density (Land 2015). To bring stimuli of interest in front of the fovea, these species are more likely to exhibit specialized eye or head movements

(Land 2015) than animals without fovea. For example, frogs have retinas with nearly uniform cell distribution (Aho 1997), and rarely shift their heads and eyes (Dieringer and Prechet 1982). In many granivorous and insectivorous birds, the retinal area of highest resolution is directed around a visual scene using characteristic head movements, while humans and higher primates use combined eye and head movements to keep the fovea trained on objects of interest (Land 2015). Similarly, stomatopods use rapid eye movement routines to examine objects with the area of heightened acuity within their stalked compound eyes (Marshall et al. 2014).

In addition to retinal topography, retinal shape can play a role in the evolution of specialized movements of the head or eyes. Some invertebrates have narrow retinas and use scanning behaviors to sample their environments more broadly. Diving-beetle larvae, which possess a pair of tubular stemmata with linear retinas, extend their visual field by pivoting their bodies up and down before striking prey (Buschbeck et al. 2007). Copepod crustaceans also perform scanning movements with their eyecups, containing a line of only 5-8 photoreceptors (Land 1988), and heteropod molluscs perform sweeping motions with their narrow, ribbon-like retinas (Land 1982).

Jumping spiders, well-known for their visually guided courtship and predatory behavior (Harland & Jackson 2012), sample their environment using narrow, vertical boomerang-shaped retinas (Land 1969b). These retinas of the antero-median eyes (AMEs) possess the best spatial acuity known for any terrestrial vertebrate (Warrant and McIntyre 1993), but they are very small and can only view a small area of the visual field at any given time. However, the field of view is extended because the retinas are located at the back of a long, moveable eye tube located inside the spider's cephalothorax. The

motions of these tubes are directed by the immobile antero-lateral eyes (ALEs) (Jakob et al. 2018), which have much broader fields of view (Homann 1928) and are excellent motion detectors (Zurek and Nelson 2012). Two main types of movement by the principal eyes have been described (Land 1969a): displacement, where the retinas are moved along the dorso-ventral or latero-medial planes, and torsion, in which the retinas rotate around a central axis. Using these basic kinds of movement, retinas can engage in four classes of activities: spontaneous activity, saccades, tracking, and scanning (Land 1969a, Harland and Jackson 2012). Scanning is the most complex class of movement (Harland and Jackson 2012), consisting of both displacement and torsional movement within the visual field of a stimulus.

A longstanding hypothesis (Land 1969a, Land and Nilsson 2012) about the function of scanning behavior in jumping spiders is that it helps the animal to identify important shapes and angles, for example the shape of a conspecific or the specific angle of a mosquito's legs. Scanning routines have not yet been well characterized, but are quite slow, and our preliminary observations using a custom-built spider eyetracker (Canavesi et al. 2011, Jakob et al. 2018) show that spiders engage in periods of scanning lasting several minutes when viewing complex static stimuli, such as a cricket silhouette or a forward-facing wasp. Thus, we hypothesize that it takes a significant amount of time for spiders to gather information about spatial detail via scanning. This hypothesis is aligned with previous research that indicates that spiders are unable to distinguish between a moving cricket silhouette and a moving rectangle, even when motivated with aversive conditioning (Bednarski et al. 2012). In that study, spiders in an arena oriented toward a moving cricket silhouette and a moving rectangle stimulus with comparable

frequency, even when trained to associate one stimulus with an electric shock. In contrast, spiders easily discriminated between a moving cricket and a still cricket, with 100% of the subjects orienting toward the moving stimulus.

Using a spider eyetracker, we showed jumping spiders videos of cricket silhouettes moving across the screen at varying speeds. We investigated whether spiders scan slow-moving or still cricket silhouettes more than fast-moving cricket silhouettes by measuring the overlap of the retinas with the stimulus field, and the amount of rotational movement (torsion) performed by the retinas while within the field of the stimulus. If spiders scan fast-moving stimuli less than slow-moving or still stimuli, they may be constrained in collecting detailed spatial information.

C. Materials and Methods

We tested 11 adult female *Phidippus audax* jumping spiders, captured using sweep nets and vials from fields and metal structures in Hampshire County, MA, USA. Spiders were housed in a lab kept at 25° C and with a 16 L : 8 D light cycle, and kept in individual plastic boxes (18 x 13 x 10 cm). They were provided a stick, a hollow black tube, and plastic foliage for habitat enrichment (Carducci and Jakob 2000). Spiders were fed crickets (*Acheta domesticus*) once weekly and provided with water *ad libitum*.

We used a specialized salticid-specific eyetracker (Jakob et al. 2018, Canavesi et al. 2011) to map the changing position of spiders' principal eye retinas as they viewed stimuli on a projector screen. The procedures were identical to those in Jakob et al. 2018, with exceptions as noted.

During a trial, individual spiders were tethered using a plastic microbrush

(Easyinmile dental disposable 38 microapplicator brush) attached to the cephalothorax using a mixture of gum rosin (Acros Organics) and beeswax (Stackich) (Jakob et al. 2018). The waxed microbrush was then painted with blackboard paint (Americana Chalkboard Paint) to eliminate glare from the infrared light.

Once in the eyetracker, spiders remained tethered for the entire trial and viewed a cricket silhouette (170x50 pixels) moving across the projector screen at 4 different speeds: fast (330 pixels/sec), medium (120 pixels/sec), slow (60 pixels/sec), and completely still. This stimulus was constructed in Processing (v. 2.2). We presented each speed treatment for 45 seconds to each spider in random order, with 3 minutes of rest (a blank, dim gray screen) in between.

Trials were video-recorded, and videos of the retinas were overlaid and aligned with stimulus videos. To quantify how well the retinas followed each stimulus in each treatment, we measured the average overlap between the retinas and the stimulus in pixels across trials, so that each spider generated a single average mean for each stimulus. To quantify the extent to which spiders scanned the stimulus, we calculated the amount of torsion using two measures: the change in retinal angle when the retinas overlapped with the stimulus, and percent change in retinal direction when retinas overlapped with the stimulus. Each spider and stimulus combination generated an average for frames in which there was overlap with the stimulus.

Retinal data was scored by first overlaying retinal videos with stimulus videos, where we set the stimulus video at 50% opacity in Final Cut Pro X on an iMac. We compressed these overlaid videos and exported them as image stacks (10 frames/sec). We then imported these images into ImageJ where we used the MTrackJ plugin to mark three

points on each retina and one point on the stimulus, frame by frame (see Jakob et al. 2018 for a more detailed description). These $x y$ coordinates were exported to Excel and then run through a custom R program that calculated the overlap in pixels between the retinas and the stimulus image. We also exported the coordinate data to Excel, where we calculated the angle of each retina in each frame.

Using these inputs, we measured the two following variables. (1) The average rotation of each retina as the absolute value of the angle change from frame to frame. We calculated this value over the course of whole trials as a measure of general activity, as well as only when the retinas overlapped with the stimulus as a measure of exploration of the stimulus itself. (2) The number of times during a trial that the retina changed direction of movement (e.g., moving counterclockwise and then clockwise). We counted the percentage of frame sequences in which there was a direction change when the retinas overlapped and did not overlap with the stimulus. Each spider generated one number for each stimulus speed.

Because spiders' attention can diminish over the course of a trial, we took each measure over the entire trial and also only for the first complete pass of the stimulus across the screen.

We tested the influence of the two independent variables (spider identity and stimulus speed) on the dependent variables (amount of overlap in pixels, retinal angle change, and retinal directional change) in an ANOVA.

D. Results

We found that stimulus speed had a significant effect on the percentage of retinal overlap in pixels, with spiders less frequently directing their retinas toward the fastest-

moving stimulus compared to the other three speeds (whole model: $F_{16,54}=3.93$, $P = 0.0003$; spider ID: $F_{13,54}=1.77$, $P < 0.09$; speed: $F_{3,54}=13.31$, $P < 0.0001$) (Fig. 2.1). This trend was also reflected in the analysis of the second pass of the stimulus only (whole model: $F_{16,54}=3.42$, $P = 0.0009$; spider ID: $F_{13,54}=0.99$, $P = 0.47$; speed: $F_{3,54}=14.01$, $P < 0.0001$) (Fig. 2.1).

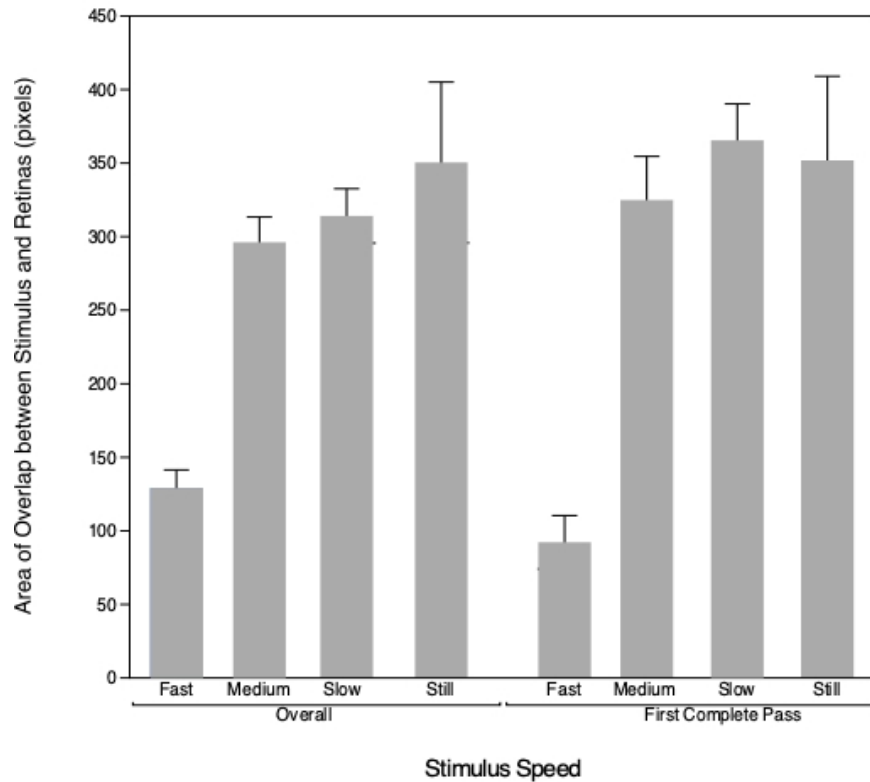


Figure 2.1. The effect of stimulus speed on the overlap of the retinas with the stimulus.

Overall, we found little evidence for an effect of stimulus speed on torsion of the retinas. Measured over the whole trial, there was no significant effect of speed on the average absolute angle change across both retinas, both during entire trials ($F_{16,53}=1.13$, $P < 0.37$) and when the retinas overlapped with the stimulus ($F_{16,53}=1.56$, $P < 0.13$) (Fig. 4).

These patterns were also when I analyzed only the first complete pass of the stimulus (whole pass: $F_{16,53}=1.30$, $P = 0.25$; overlap only: $F_{16,53}=1.13$, $P = 0.36$) (Fig. 2.2).

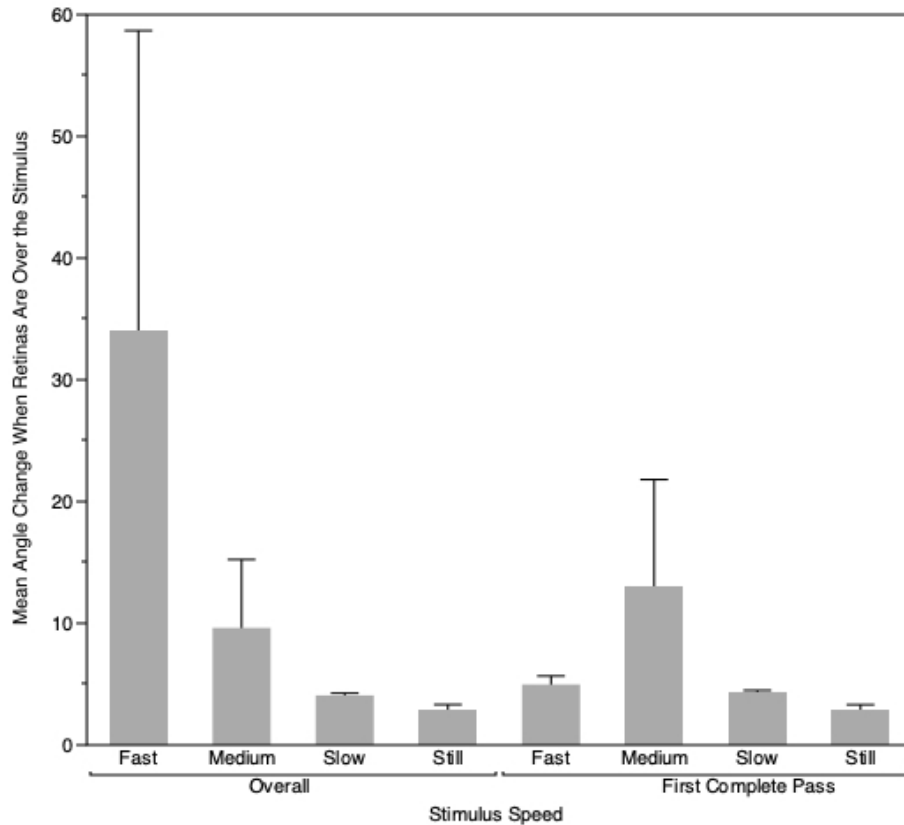


Figure 2.2. The effect of stimulus speed on the average angle change of both retinas.

In the analysis of whole trials, there is a trend toward a significant effect of speed on the change in direction of the retinas when the retinas are over the stimulus (whole model: $F_{16,54}=1.90$, $P = 0.053$; spider ID: $F_{13,54}=1.36$, $P = 0.22$; speed: $F_{3,54}=4.75$, $P < 0.007$) (Fig. 2.3). However, contrary to expectations, there was less directional change while the retinas overlap with a stationary stimulus compared to a moving stimulus (speed: $F_{3,54}=4.75$, $P < 0.007$). This pattern disappeared in the analysis of the first full pass of the stimulus only ($F_{16,53}=0.88$, $P < 0.60$).

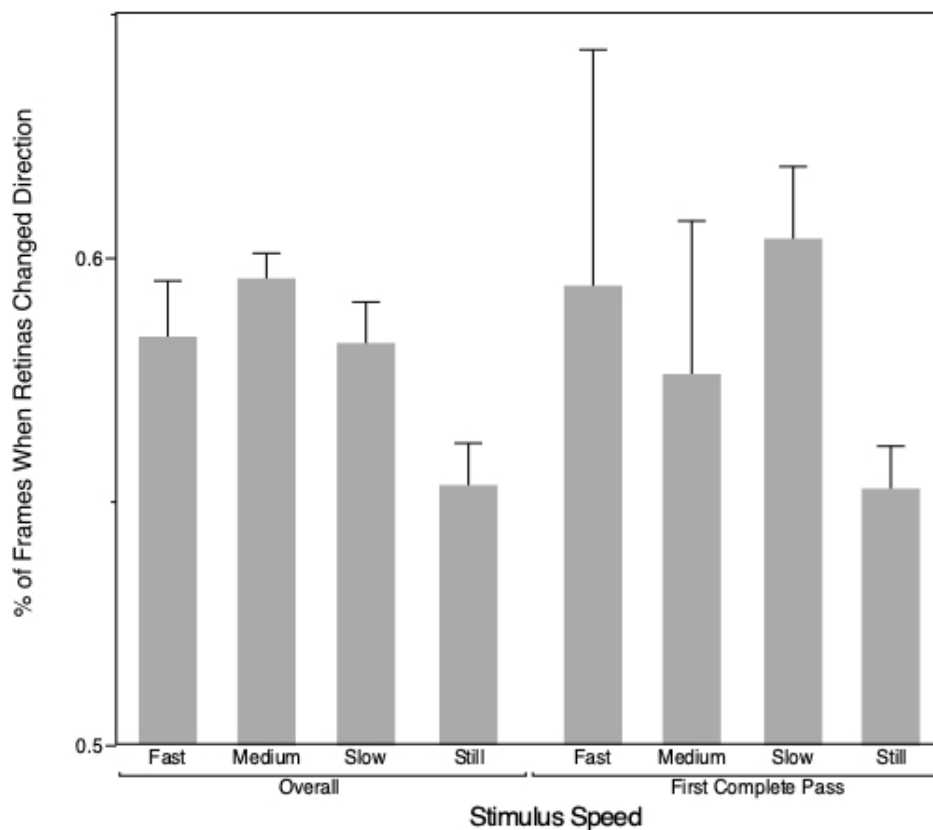


Fig 2.3. The effect of stimulus speed on angular directional change of retinas.

E. Discussion

Our results indicate that spiders spend less time examining quickly moving stimuli with their principal eye retinas than they do more slowly moving or still images (Fig. 2.1). It is unclear whether this trend is due to spiders being physically unable to follow our fast stimulus (moving across the screen at 330 pixels/sec), or if they are using their ALEs, which are specialized motion detectors (Zurek and Nelson 2012, Jakob et al. 2018), to monitor these stimuli. Visual input by the ALEs alone could constrain the amount of detail that could be extracted from a stimulus, as they are less specialized for high resolution vision than the principal eyes. They do, however, possess more densely

packed, optically isolated photoreceptors than the two other pairs of secondary eyes, supporting high spatial acuity (Zurek and Nelson 2012). Future researchers could use a simple experiment to search for the existence of a threshold for speed processing by the principal eyes; perhaps a physiological or perceptual limit constrains the ability of the retinas to track stimuli of a certain velocity.

Because we found no significant effect of stimulus speed on the amount of retinal angle change (Fig. 2.2), we cannot draw any conclusions about the effect of speed on scanning behavior. Furthermore, our analysis of the effect of stimulus speed on angular directional change of the retinas shows that spiders rotate their retinas less when they are viewing still images of cricket silhouettes (Fig. 2.3). This finding countered our expectations and is distinctly different from pilot data collected in the eyetracker where spiders extensively scanned still images of crickets and wasps. Possible explanations are that the group of female spiders used in this experiment was elderly and less motivated to eat than spiders used during the collection of pilot data, and that spiders are more interested in stationary stimuli that exhibit local motion. *Phidippus audax* has been shown to prefer local and global motion together over global motion alone, more often approaching videos depicting natural cricket motion than those depicting a cricket snapshot moving across a screen (Bednarski et al. 2012). Similarly, ongoing work with species of *Habronattus* jumping spiders in the eyetracker indicates that females extensively attend to images of courting males that are primarily stationary except for flicking legs. Future studies should investigate the role of local motion within a globally stationary stimulus in eliciting retinal scanning.

Future research should also aim for a deeper understanding of the abilities of the ALEs, which are likely involved in other aspects of visual processing (Forster 1979, Zurek et al. 2010) besides motion detection, as suggested by their binocular overlap and central acute zone (Homann 1928, Land 1985). In addition, until now, the placement of the acute zone at the “elbow” of the boomerang-shaped principal-eye retina has received the most attention. Our observations of spiders in the eyetracker suggest that spiders also appear to momentarily place the distal “tips” of these retinas over stimuli. The function of this and other behaviors of spider eyes, and how these behaviors relate to the peculiar boomerang shape of salticid retinas, remains to be discovered.

BIBLIOGRAPHY

- Aho, A. C. (1997). The visual acuity of the frog (*Rana pipiens*). *Journal of Comparative Physiology A: -Sensory Neural and Behavioral Physiology*, 180(1), 19-24.
- Barth, F. G. (2001). *A Spider's World: Senses and Behavior*. Springer-Verlag, Berlin Heidelberg.
- Bednarski, J. V., Taylor, P., & Jakob, E. M. (2012). Optical cues used in predation by jumping spiders, *Phidippus audax* (Araneae, Salticidae). *Animal Behaviour*, 84(5), 1221-1227.
- Blumstein, D. T. (1998). Quantifying predation risk for refuging animals: A case study with golden marmots. *Ethology*, 104(6), 501-516.
- Brick, O. (1998). Fighting behaviour, vigilance and predation risk in the cichlid fish *Nannacara anomala*. *Animal Behaviour*, 56, 309-317.
- Buschbeck, E. K., Sbita, S. J., & Morgan, R. C. (2007). Scanning behavior by larvae of the predacious diving beetle, *Thermonectus marmoratus* (Coleoptera : Dytiscidae) enlarges visual field prior to prey capture. *Journal of Comparative Physiology A: Neuroethology Sensory Neural and Behavioral Physiology*, 193(9), 973-982.

- Canavesi, C., Long, S., Fantone, D., Jakob, E., Jackson, R. R., Harland, D., et al. (2011, Aug 22). *Design of a retinal tracking system for jumping spiders*. Paper presented at the Conference on Novel Optical Systems Design and Optimization XIV, San Diego, CA.
- Carducci, J. P., & Jakob, E. M. (2000). Rearing environment affects behaviour of jumping spiders. *Animal Behaviour*, *59*, 39-46.
- Corrigan, B. W., Gulli, R. A., Doucet, G., & Martinez-Trujillo, J. C. (2017). Characterizing eye movement behaviors and kinematics of non-human primates during virtual navigation tasks. *Journal of Vision*, *17*(12), 22.
- Dukas, R., & Kamil, A. C. (2000). The cost of limited attention in blue jays. *Behavioral Ecology*, *11*(5), 502-506.
- Dieringer, N., & Precht, W. (1982). Compensatory head and eye-movements in the frog and their contribution to stabilization of gaze. *Experimental Brain Research*, *47*(3), 394-406.
- Finch, O. D. (2005) The parasitoid complex and parasitoid-induced mortality of spiders (Araneae) in a Central European woodland. *Journal of Natural History*, *39*, 2339-2354.

- Forster, L. M. (1979) Visual mechanisms of hunting behavior in a jumping spider (Araneae, Salticidae). *New Zealand Journal of Zoology*, 6, 79-93.
- Giurfa, M., & Menzel, R. (1997). Insect visual perception: complex abilities of simple nervous systems. *Current Opinion in Neurobiology*, 7(4), 505-513.
- Harland, D.P., Li, D., and Jackson, R.R. (2012). *How jumping spiders see the world*. In *How Animals See the World*, O.F. Lazareva, T. Shimizu and E.A. Wasserman, eds. (Oxford: Oxford University Press), pp. 133-163.
- Homann, H. (1928). Beiträge zur Physiologie der Spinnenaugen. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*. 7(2), pp. 201-268.
- Humphrey, B., W. S. Helton, C. Bedoya, Y. Dolev & X. J. Nelson. (2018). Psychophysical investigation of vigilance decrement in jumping spiders: overstimulation or understimulation? *Animal Cognition*, 21, 787-794.
- Jakob, E. M., Long, S. M., Harland, D. P., Jackson, R. R., Carey, A., Searles, M. E., et al. (2018). Lateral eyes direct principal eyes as jumping spiders track objects. *Current Biology*, 28(18), R1092-R1093.

- Krause, J., & Godin, J. G. J. (1996). Influence of prey foraging posture on flight behavior and predation risk: Predators take advantage of unwary prey. *Behavioral Ecology*, 7(3), 264-271.
- Land, M. F. (1969a). Movements of the retinae of jumping spiders (Salticidae – Dendryphantinae) in response to visual stimuli. *Journal of Experimental Biology*, 51(2), 471-493.
- Land, M. F. (1969b). Structure of retinae of principal eyes of jumping spiders (Salticidae – Dendryphantinae) in relation to visual optics. *Journal of Experimental Biology*, 51(2), 443-470.
- Land, M. F. (1982). Scanning eye-movements in a heteropod mollusc. *Journal of Experimental Biology*, 96(FEB), 427-430.
- Land, M. F. (1985) Fields of view of the eyes of primitive jumping spiders. *Journal of Experimental Biology*, 119, 381-384.
- Land, M. F. (1988). The functions of eye and body movements in *Labidocera* and other copepods. *Journal of Experimental Biology*, 140, 381-391.
- Land, M. F. (1995). The functions of eye movements in animals remote from man. *Eye Movement Research: Mechanisms, Processes and Applications*, 6, 63-76.

Land, M. F., & Hayhoe, M. (2001). In what ways do eye movements contribute to everyday activities? *Vision Research*, 41(25-26), 3559-3565.

Land, M. F., & Nilsson, D. E. (2012). Animal Eyes, Second Edition. *Animal Eyes, Second Edition*, 1-271.

Land, M. F. (2015). Eye movements of vertebrates and their relation to eye form and function. *Journal of Comparative Physiology a-Neuroethology Sensory Neural and Behavioral Physiology*, 201(2), 195-214.

Long, S. M. (2016). *Spider brain morphology and behavior* (Doctoral dissertation). Retrieved from Dissertations and Theses at Scholarworks@UMass Amherst. 707.

Marshall, N. J., Land, M. F., & Cronin, T. W. (2014). Shrimps that pay attention: saccadic eye movements in stomatopod crustaceans. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 369(1636), 8.

Menda, G., P. S. Shamble, E. I. Nitzany, J. R. Golden & R. R. Hoy. (2014). Visual Perception in the Brain of a Jumping Spider. *Current Biology*, 24, 2580-2585.

- Morawetz, L., & Spaethe, J. (2012). Visual attention in a complex search task differs between honeybees and bumblebees. *Journal of Experimental Biology*, 215(14), 2515-2523.
- Rees, G., Frith, C. D., & Lavie, N. (1997). Modulating irrelevant motion perception by varying attentional load in an unrelated task. *Science*, 278(5343), 1616-1619.
- Schlinger, E. I. (1987). The biology of Acroceridae (Diptera): true endoparasitoids of spiders. In W. Nentwig (Ed.), *Ecophysiology of Spiders* (pp. 319-327). Springer-Verlag.
- Spaethe, J., Tautz, J., & Chittka, L. (2006). Do honeybees detect colour targets using serial or parallel visual search? *Journal of Experimental Biology*, 209(6), 987-993.
- Spano, L., Long, S. M., & Jakob, E. M. (2012). Secondary eyes mediate the response to looming objects in jumping spiders (*Phidippus audax*, Salticidae). *Biology Letters*, 8(6), 949-951.
- Strausfeld, N. J. & F. G. Barth. (1993). 2 visual systems in one brain – neuropils serving the secondary eyes of the spider *Cupiennius salei*. *Journal of Comparative Neurology*, 328, 43-62.

- Strausfeld, N. J., P. Weltzien & F. G. Barth. (1993) visual systems in one brain – neuropils serving the secondary eyes of the spider *Cupiennius salei*. *Journal of Comparative Neurology*, 328, 63-75.
- Strausfeld, N. J. (2012). *Arthropod brains: Evolution, functional elegance, and historical significance*. Cambridge, Mass: Belknap Press of Harvard University Press.
- Tatler, B. W., Wade, N. J., Kwan, H., Findlay, J. M., & Velichkovsky, B. M. (2010). Yarbus, eye movements, and vision. *I-Perception*, 1(1), 7-27.
- van Swinderen, B., & Greenspan, R. J. (2003). Saliency modulates 20-30 Hz brain activity in *Drosophila*. *Nature Neuroscience*, 6(6), 579-586.
- Warrant, E. J., & McIntyre, P. D. (1993). Arthropod eye design and the physical limits to spatial resolving power. *Progress in Neurobiology*, 40(4), 413-461.
- Wiederman, S. D., & O'Carroll, D. C. (2013). Selective Attention in an Insect Visual Neuron. *Current Biology*, 23(2), 156-161.
- Yorzinski, J. L., Patricelli, G. L., Babcock, J. S., Pearson, J. M., & Platt, M. L. (2013). Through their eyes: selective attention in peahens during courtship. *Journal of Experimental Biology*, 216(16), 3035-3046.

Yorzinski, J. L., Patricelli, G. L., Bykau, S., & Platt, M. L. (2017). Selective attention in peacocks during assessment of rival males. *Journal of Experimental Biology*, 220(6), 1146-1153.

Yorzinski, J. L., Patricelli, G. L., Platt, M. L., & Land, M. F. (2015). Eye and head movements shape gaze shifts in Indian peafowl. *Journal of Experimental Biology*, 218(23), 3771-3776.

Zurek, D. B., A. J. Taylor, C. S. Evans & X. J. Nelson. (2010). The role of the anterior lateral eyes in the vision-based behaviour of jumping spiders. *Journal of Experimental Biology*, 213, 2372-2378.

Zurek, D. B., & Nelson, X. J. (2012). Hyperacute motion detection by the lateral eyes of jumping spiders. *Vision Research*, 66, 26-30.