The role of the anterior lateral eyes in the vision-based behaviour of jumping spiders

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SUMMARY

Jumping spiders, or salticids, sample their environment using a combination of two types of eyes. The forward-facing pair of 'principal' eyes have narrow fields of view, but exceptional spatial resolution, while the two or three pairs of 'secondary' eyes have wide fields of view and function especially well as motion analysers. Motion detected by the secondary eyes may elicit an orienting response, whereupon the object of interest is examined further using the high-acuity principal eyes. The anterior lateral (AL) eyes are particularly interesting, as they are the only forward-facing pair of secondary eyes. In this study, we aimed to determine characteristics of stimuli that elicit orienting responses mediated by the AL eyes. After covering all eyes except the AL eyes, we measured orienting responses to dot stimuli that varied in size and contrast, and moved at different speeds. We found that all stimulus parameters had significant effects on orientation propensity. When tethered flies were used as prey, we found that visual information from the AL eyes alone was sufficient to elicit stalking behaviour. These results suggest that, in terms of overall visual processing, the relevance of spatial vision in the AL eyes has been underestimated in the literature. Our results also show that female spiders are significantly more responsive than males. We found that hunger caused similar increases in orientation propensity in the two sexes, but females responded more often than males both when sated and when hungry. A higher propensity by females to orient toward moving objects may be related to females tending to experience higher nutritional demands than males.

Key words: movement, vision, Salticidae, decision making, cognition, psychophysics.

INTRODUCTION

The quantification of perceptual thresholds allows for the assessment of the abilities and limitations of an animal's sensory system. It also permits an understanding of how brains 'filter' an overabundance of sensory information and provides insight into how the brain allocates 'priorities'. Jumping spiders (Salticidae) are a particularly interesting group of animals in which to investigate perceptual processes because of their exceptional cognitive attributes, including the ability to make detours while losing sight of the target, and other examples of forward planning (Harland and Jackson, 2004; Jackson and Pollard, 1996; Tarsitano and Jackson, 1997). These feats are largely achieved as a result of their outstanding vision, with spatial acuity that is vastly superior to that of other animals of comparable size (Land, 1985; Land and Nilsson, 2002).

The salticid visual system is distinct in being a modular system featuring highly specialized and anatomically distinct pairs of eyes: two pairs of forward-facing eyes, the anterior median (AM) and anterior lateral (AL) eyes, and the side-facing posterior median (PM, reduced in most species) and posterior lateral (PL) eyes (Land, 1985). Following convention, the last three pairs of eyes will hereafter be collectively referred to as 'secondary eyes'. Together with the AM eyes ('principal eyes'), these form an intricate modular visual system whose subsystems provide their bearer with the visual information needed. The AM eyes provide outstanding spatial acuity (as low as 0.04 deg) and depth of field, but the high-acuity regions on the AM retinae are limited to fields of view of less than 1 deg and contain no more than a few hundred receptors (Blest et al., 1990; Land, 1969a; Williams and McIntyre, 1980). Jumping spiders bring

the AM eyes to bear by orienting towards moving stimuli that are detected by the secondary eyes (Land, 1971). This is known as orienting behaviour.

Of the two forward-facing pairs of eyes (AL and AM), the AL eyes have a larger and also overlapping field of view [from *ca*. –25 to 60 deg, depending on species (Land, 1985)]. The AL eyes are very effective at detecting moving objects, and, like the PL eyes, mediate orientation turns (Land, 1971; Duelli, 1978). There is some evidence, however, that the AL eyes play a role in quickly categorizing moving objects and in the initiation of appropriate responses such as chasing behaviour, including prey capture, even when the principal eyes are occluded (Forster, 1979). Forster's results suggest that these eyes support high-resolution spatial vision (Forster, 1979), as is also suggested by the fact that receptors in the retinae of salticid AL eyes form a dense regular pattern and have forward-facing acute zones (O'Carroll, 1989). Functionally, the AL eyes may act as a bridge between the AM eyes (higher spatial acuity, narrow field of view) and the PL eyes (lower spatial acuity, wide field of view).

In order to avoid orienting unnecessarily to irrelevant stimuli, the secondary eyes must be able to discern relevant from irrelevant motion, as is typical of motion detection in visual systems (Nordström et al., 2006). This problem is nicely illustrated by our study species, *Servaea vestita* Koch. This cryptic bark-dwelling salticid is found only on *Eucalyptus* trees. In a habitat dominated by peeling bark, moving foliage and the complex interplay of shadows these create, *S. vestita* needs to be able to pick out specific types of stimuli, such as potential mates and prey.

Salticids are known to respond to computer-generated visual stimuli with behaviour similar to that elicited by the equivalent real stimulus (Nelson and Jackson, 2006). Using computer-generated stimuli, we tested *S. vestita* that were fully blinded except for the AL eyes to determine the characteristics of visual stimuli that would elicit an orientation response.

Visual perception has been studied in a variety of animals, from primates (Britten et al., 1992; Gescheider, 1997; Valois, 1974), to insects (Plateau, 1888; Hassenstein, 1951; Horridge et al., 1992; Prete and Mahaffey, 1993; Prete et al., 2002) and spiders (Duelli, 1978; Land, 1971). Despite work spanning over a century, most studies have only addressed perception in a single sex. There is reason to believe that jumping spiders may exhibit differences in their perceptual ability based on sex. For example, adult male jumping spiders are less prone to complete behavioural tasks in laboratory experiments (Jackson and Hallas, 1986; Jackson and Pollard, 1996). Males also feed less often than females, and consume less of their prey when feeding (Givens, 1978). Whether the orientation response of salticids is a spontaneous reflex unaffected by internal states, or whether it is affected by a physiological state of heightened interest has never been investigated. Given the lower foraging investment by male jumping spiders, we hypothesized that orienting responses would be affected by sex and by hunger level.

MATERIALS AND METHODS
General

Adults of *S. vestita* were kept individually in cylindrical transparent plastic jars (diameter 115 mm, height 125 mm), with a cotton roll inserted into a hole made in the bottom of the jar and extending into a cup of water that was topped-up as needed, providing constant humidity. The cages had two additional holes of 10 mm diameter at the top, one covered with cotton gauze for ventilation and another (the 'feeding hole') which was plugged with a cork. Cages were enriched with sticks that were inserted through folded card within which *S. vestita* could hide and build nests. Adult *S. vestita* were fed weekly with three house flies (*Musca domestica*) or three fruit flies (*Bactrocera tryoni*) and a variety of field-caught dipterans (mass similar to one house fly). Cages were cleaned the day before feeding. As preliminary testing showed that time of day did not significantly affect behaviour (overall orientation propensity, am 0.21±0.04, pm 0.22±0.04, means ± s.e.m.; independent samples *t*-test, *t*=0.244, *P*=0.814, *N*=24 spiders), tests were carried out between 08:00 and 18:00 h. Lighting in the laboratory consisted of 12 36 W fluorescent bulbs and four 150 W floodlights on a 12 h light/dark cycle with lights on at 07:00 h. Temperature was kept between 22 and 27°C.

Moving dot tests

Using a stereomicroscope we covered all eyes except the AL eyes with dental silicone (Coltène/Whaledent President light body polyvinyl siloxane, Coltène/Whaledent AG, Altstätten, St Gallen, Switzerland), which sets to become a smooth elastomer within minutes of mixing its two components. This material is opaque and non-toxic (Mandikos, 1998) and binds to the eyes so that the spider cannot remove it with the legs or pedipalps. Using fine forceps, the material can be easily removed without apparent damage to the cornea or leaving residue. Spiders were restrained by placing them in a large diameter plunger with a foam base. The outer tube of this plunger was a plastic vial in which numerous small holes had been made. This allowed us to position the spider such that only its cephalothorax protruded from the tube, while restraining it without observable adverse effects.

We tested 52 *S. vestita* adults (26 females, 26 males). Half of the males and half of the females were tested the day after feeding, while the other half were tested 7 days after feeding. Test spiders, with all eyes other than the AL eyes covered, were held in place using methods adapted from Hassenstein (Hassenstein, 1951) and Land (Land, 1971). A 3 mm³ cork cube connected to a thin wire was attached to the cephalothorax with a drop of bee's wax. This makes it possible to suspend the spider from a crocodile clip on a flexible arm, which can be moved to the desired location. Suspended spiders were positioned 150 mm from the centre of two adjoining screens, facing the joint (Fig. 1). In this position, the screens filled the complete field of vision of the AL eyes (D.B.Z. and X.J.N., unpublished field of view data). Suspended spiders were given a 160 mg polystyrene ball (diameter 15 mm) with crosshair markings, which they readily held on to. While heavier than the average weight of an adult spider (adult female 64.1±16.6 mg, *N*=45; adult male 56.8±23.4 mg, *N*=26; means ± s.d.), the ball was light enough for the spider to turn easily, and no signs of fatigue were evident in preliminary trials.

Previous experiments with jumping spiders have shown that life-like video and 3D animation stimuli elicit similar reactions to natural stimuli (Clark and Uetz, 1990; Harland and Jackson, 2002; Nelson and Jackson, 2006). We presented moving gratings to spiders in preliminary trials, but these failed to elicit orientation turns. However, spiders readily attempted to track small targets. The gratings most likely were regarded as background motion. Consequently, in a setup comparable to those of Land (Land, 1971), Duelli (Duelli, 1978) and Komiya and colleagues (Komiya et al., 1988), we used dot stimuli on a featureless background in subsequent experiments.

We generated horizontally moving single dots that moved from the left or the right periphery of the AL eyes' field of view (60 deg) towards the point at which the two screens adjoin. The dots differed in size, speed and contrast. Based on observations made in preliminary trials, we chose a range of values spanning from below threshold levels to above saturation for testing. We used five values for each parameter, and presented each spider with all combinations of these values (i.e. there were a total of 125 unique dot stimuli per spider). Order and side of presentation of the stimuli were randomized. After the spider had been allowed to get used to the featureless grey screen for at least 5 min, stimuli were presented every 2 min and orienting responses to stimuli were scored.

Typical orienting responses consist of a rapid turn (mean ± s.d.; 595±242 deg s⁻¹, *N*=8 spiders; *n*=25 experiments) toward a stimulus, followed either by crouching or by further turns to track the moving stimulus. In our experiment, an orienting response led to a sudden, rapid spin of the ball in the direction opposite to that of the stimulus. Because of their speed and discrete nature, orientation movements are easily distinguished from other salticid movements (such as
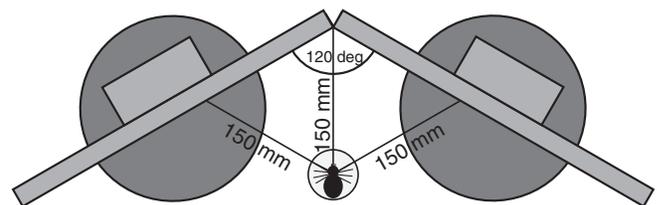

Fig. 1. Arrangement of stimulus presentation screens when viewed from above. Spider facing intersection of screens at a distance of 150 mm. Spider not to scale.

walking or turning) and were scored as binary responses. Orienting behaviour very rarely occurs spontaneously. As a baseline, orientation turns in the absence of dot stimuli (i.e. only featureless grey background) were scored from 15 video recordings of 10 s length per spider.

Dot stimuli were generated using VPixx V2.36 (VPixx Technologies Inc., Montreal, QC, Canada) created on a Mac Pro (2×2.8 GHz Quad Core Xeon, 4 GB RAM) and a MacBook Pro (2.4 GHz Core 2 Duo, 4 GB RAM) (Apple Computer Inc., Cupertino, CA, USA). Each computer was connected to one of the experimental screens *via* DVI cables. Two 17 in TFT screens (Samsung 743B, resolution 1280 pixels×1024 pixels, 75 Hz, response time 5 ms; Samsung Electronics, Seoul, South Korea) were positioned at an angle of 120 deg with respect to each other on a vibration isolation table (Kinetic Systems, Boston, MA, USA). The screens were colour calibrated and brightness levels were adjusted with an Eye One Display V.2 colorimeter (X-Rite Inc., Grand Rapids, MI, USA) controlled using ColorHCFR v.2.1 (HCFR Colorimeter team, Paris, France) on an external PC. Stimulus contrast was defined as the difference between the luminance of the stimulus and the background, divided by the luminance of the background (Weber contrast). Both stimulus and background were generated in shades of grey, using the Lxy colour space. The stimulus was always darker than the background, as relevant objects moving into the field of view of the AL eyes are usually darker than the background (Duelli, 1978). For a spider 150 mm away from the screen, 1 pixel was 0.1 deg wide. The experimental setup was filmed from directly behind the spider using a Sony DCR HC52E DV camera (Sony Corporation, Minato, Tokyo, Japan), recording directly into iMovie '08 (Apple Computer Inc.) *via* FireWire 400. This setup did not permit testing with extremely slow- or fast-moving dots. The screen's resolution limited the smoothness of extremely slow stimulus motion such that its movement became saltatory from pixel to pixel every few seconds, rather than the smoother motion occurring at medium speeds. Very fast speeds were limited by the screen's refresh rate of 75 Hz. However, orientations to the extremely fast movements that were testable were rare, giving us confidence that the ranges used here were adequate.

Ramp trials

The objective was to determine the predatory responses that could be elicited when the only visual input for the spider was from the AL eyes and to investigate how motivation might affect attacking and stalking. For this, we placed two fruit flies in spider cages on the first day and subsequently checked for feeding in each cage every 5 min. Twenty-three females and 15 males fed; these were then used for paired tests on days 2 and 8.

The testing apparatus was a plywood ramp (32 cm long, 8 cm wide, incline 20 deg) with a triple coating of polyurethane. The ramp was placed within a cylinder of white cardboard (60 cm high) to minimize external visual stimulation, and was lit by two 60 W incandescent lamps in addition to standard laboratory lighting. For testing, a live house fly was affixed to a piece of transparent plastic by the two hind legs using bee's wax, and placed 5 cm from the top end of the ramp. The fly could still move and thereby potentially elicit predatory responses from *S. vestita*. The test spider was placed at the lower end of the ramp, at a distance of 25 cm from the fly, covered by a 40 mm Petri dish. This allowed the spider to calm down for a few minutes while providing it with visual access to the fly, as salticids are known to respond to prey seen at distances of 30 cm (Harland et al., 1999). Once the spider was on the ramp and

displayed 'relaxed' behaviour (i.e. became quiescent, started grooming), the Petri dish was lifted *via* a thread attached to the dish. The spider was then filmed (using the same camera as above) until it attacked the fly, jumped off the ramp, or the test cut-off time of 5 min was reached. Based on these recordings, we scored stalking (crouching while moving toward prey) and attack (striking or pouncing on prey) behaviour (Jackson and Pollard, 1996) as all-or-nothing responses. Spiders were not allowed to feed on the fly. The ramp was wiped with 80% ethanol after each trial in order to remove draglines and chemical cues.

Statistical methods

To analyse the effects of stimulus size, contrast and speed, as well as sex and hunger state, on orientation propensity, we used generalized estimated equations (GEE), as implemented in Stata 11 (Statacorp 2009, Stata Statistical Software: release 11; www.stata.com). This method is appropriate when the outcome variable is dichotomous and some of the observations are correlated (Burton et al., 1998), and provides population-averaged estimates of the effects (Hu et al., 1998). In the present analysis, the correlations between observations from the same spider were assumed to be exchangeable; that is, equally correlated (Burton et al., 1998). The independent variables in this analysis were stimulus size, contrast and speed, as well as spider sex and hunger level. Orientation was the dependent variable. Some of the stimulus combinations involving high speeds and low contrast produced no orientation responses. In order to provide an estimable model, two high-speed conditions (27 and 81 deg s^{-1}) and three low contrast conditions (1%, 5% and 10%) were combined.

The tested model contained the full factorial interaction for stimulus size (five levels), contrast (three levels) and speed (four levels). It also tested the main effects of sex and hunger, their two-way interaction, and the two-way interactions of sex and hunger respectively with size, contrast and speed.

Frequencies of stalking and attacking in the ramp trials were analysed using Fisher's exact test as implemented in SPSS (v. 16; Chicago, IL, USA).

RESULTS
Moving-dot tests

Spontaneous orientation (i.e. orientation in the absence of stimuli) was rare (orientation propensity, always given as mean ± s.e.m. in this section: 0.0023±0.0004, N=24, n=360). Each spider was presented with 125 dot stimuli featuring a unique combination of size, contrast and speed. Different combinations of these parameters led to different orientation propensities (Fig. 2), as indicated by the significant three-way interaction (Table 1). We found that the stimulus that evoked the strongest orientation propensity (0.9±0.0045) was a dot with a diameter of 4 deg and 40% contrast, moving at a speed of 9 deg s^{-1}. Both sex and hunger state had a significant effect on orientation propensity (Table 1; Figs 3 and 4). Overall, females were significantly more reactive than males (overall orientation propensity in females 0.263±0.011, males 0.176±0.012; χ^2_1=28.73, P<0.0005), and hungry spiders were significantly more responsive than sated spiders (overall orientation propensity in sated spiders 0.185±0.013, hungry 0.255±0.01; χ^2_1=14.14, P<0.0005). As is apparent from the slopes in Fig. 3, the way in which hunger increased responsiveness was similar in the two sexes, and no significant interaction effect was found between sex and hunger (Table 1). *A priori* tests of simple effects showed that both sexes were significantly more responsive when hungry (orientation propensity hungry *vs* not hungry was 0.305±0.01 *vs*
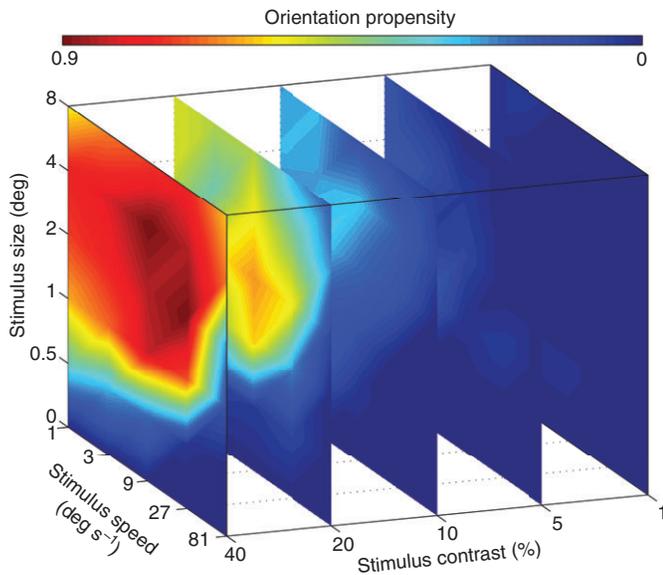
Fig. 2. Orientation propensity of spiders when horizontally moving dot stimuli with different combinations of size, speed and contrast were presented. Data for 0% contrast and speeds under 1 deg s^{-1} not shown (see Materials and methods).
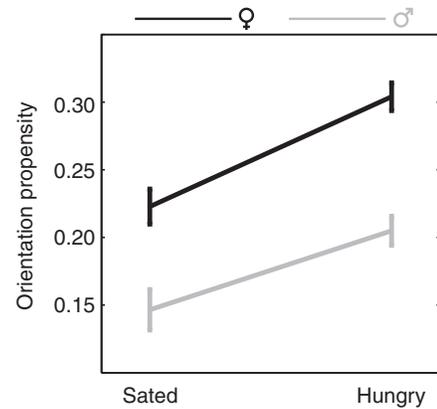

Fig. 3. Overall orientation propensity (means ± s.e.m.) of male and female jumping spiders in two hunger conditions, when horizontally moving dots were presented.

0.226±0.013 in females, χ^2_1=12.12, P=0.0005, and 0.206±0.011 vs 0.142±0.015 for males, χ^2_1=5.48, P=0.019). Females were always significantly more responsive than males in the same hunger state (orientation propensity females vs males when not hungry was 0.226±0.013 vs 0.142±0.015, χ^2_1=8.49, P=0.0036, and 0.305±0.01 vs 0.206±0.011 when hungry, χ^2_1=23.51, P<0.0005). Although not significant, a trend towards an interaction of stimulus size and spider sex was found (Table 1).

The lowest contrast that elicited orientation responses was 1% (orientation propensity 0.008±0.0016). In general, the higher its contrast, the more often the stimulus elicited a response (Fig. 2; Fig. 5A). This effect was somewhat conditional on both the size and speed of the stimuli: when the stimulus size was 0.5 deg, the effect of increasing contrast when speed was 27/81 deg s^{-1} was negligible,

and also tended to be small at other speeds. However, when dots of greater size were used, the effects of increasing contrast were uniform. It is worth noting that while the interaction between contrast and speed was not significant at 27/81 deg s^{-1} when size was 0.5 deg (χ^2_8=10.30, P=0.244), the interaction was significant at the three other speeds (0.026>P<0.0019). Preliminary experiments showed that a ceiling of 0.8 orientation propensity is reached when contrast is increased over 40% (data not shown).

Size also had a significant effect on orientation propensity (Table 1, χ^2_4=155.53, P<0.0005). This effect was non-linear, although generally speaking bigger dots led to a higher propensity to orient. At the three lowest contrast values (0.5%, 1% and 10% combined), increases in size had little effect at any speed, while at contrast values of 20% and 40% increases in size led to significantly increased orientation propensity, more sharply at lower size values, and levelling off at higher values (Fig. 5B). Overall, the maximum orientation propensity was reached with stimulus sizes between 2 and 4 deg and decreased above this size (Fig. 2).

Of the three parameters, speed had the smallest impact on orientation propensity, although this was still strongly significant (Table 1, χ^2_3=108.05, P<0.0005). Orientation propensity significantly decreased with increased speed at the lowest contrast values (0.5%, 1% and 10% combined) while at the highest contrast (40%) there was a significant increase in orientation propensity when speed was increased up to 9 deg s^{-1} (except for the very smallest stimulus size) and then a drop for the combined 27 and 81 deg s^{-1} conditions (Fig. 5C).

Ramp trials

Despite having all but the AL eyes blinded, spiders did both stalk and attack flies. The moving dot tests showed that 1 week of food deprivation significantly increased orienting responses toward dots at threshold and above. Here, we found that, at least for females, this increase in response due to changes in physiological state also was expressed in directed behaviour. Even though only a small proportion of test spiders responded, there was a significant increase in female propensity to stalk after 1 week of food deprivation (Fisher's exact test, P=0.015, sated 2, hungry 9, N=22) and a marginal non-significant increase in the propensity of attack (Fisher's exact test, P=0.082, sated 1, hungry 5, N=22). Males, on the other hand, showed minimal increases in these behaviours (stalk: Fisher's exact test, P=0.339, sated 2, hungry 3, N=13; attack: Fisher's exact test, P=0.249, sated 1, hungry 3, N=13).

Table 1. Generalized estimating equations (GEE) results indicating the effects of stimulus contrast, size and speed and spider sex and hunger level on orientation propensity

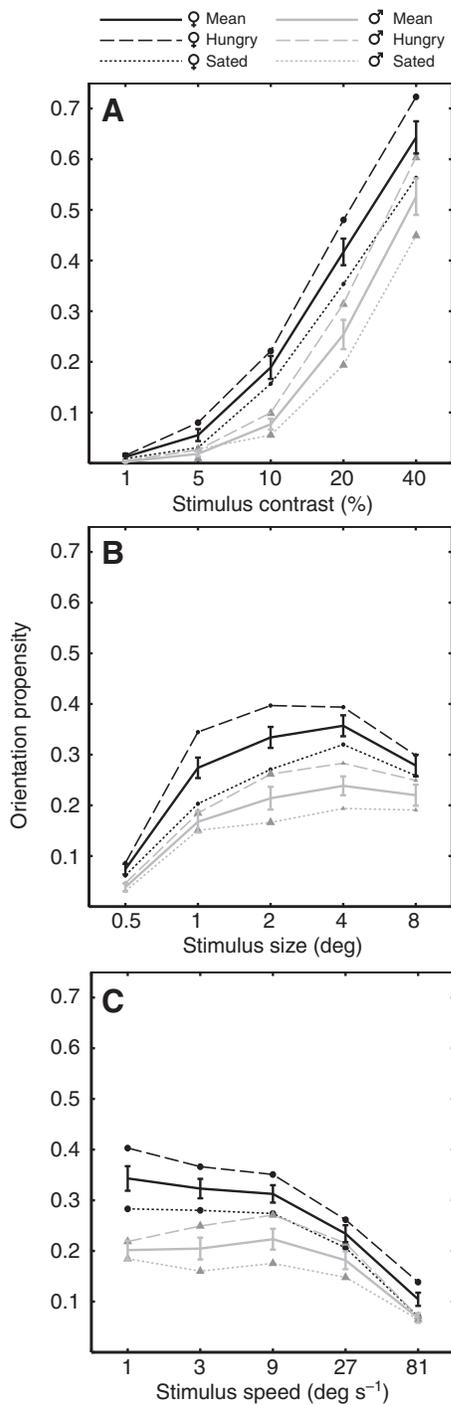| Effect	χ^2	d.f.	P
Size	155.53	4	<0.00005
Contrast	411.18	2	<0.00005
Speed	108.05	3	<0.00005
Size × contrast	18.62	8	0.017
Size × speed	69.07	12	<0.00005
Contrast × speed	60.38	6	<0.00005
Size × contrast × speed	79.55	24	<0.00005
Sex	28.73	1	<0.0005
Hunger	14.14	1	<0.0005
Sex × hunger	0.044	1	0.832
Sex × size	8.89	4	0.064
Sex × contrast	1.46	2	0.481
Sex × speed	3.52	3	0.319
Hunger × size	7.20	4	0.126
Hunger × contrast	4.55	2	0.103
Hunger × speed	3.60	3	0.308

Fig. 4. Orientation propensity of male and female spiders in two hunger conditions, when dot stimuli with varying contrasts (A), sizes (B) and speeds (C) were presented.

spatial acuity capability sufficient for directing complete predatory sequences.

In particular, the results using tethered flies on ramps corroborate previous findings on the possible dual role of the AL eyes, as without considerable spatial acuity the flies should not have elicited predatory responses. While the AL eyes of jumping spiders do not achieve the spatial acuity of the AM eyes, they do have a high acuity forward-facing fovea, coupled with a wider field of view (O'Carroll, 1989). In contrast, the role of the PL eyes appears to be particularly specialized for motion detection – their unmovable retinas contain receptors that are evenly spaced and provide wide acceptance angles (Land, 1969b; Duelli, 1978).

For *S. vestita* in nature, the salient animals most commonly encountered include small dipterans, ants, conspecific spiders and other small spiders. It is of interest that the size of these animals and speed at which they move seem to match well the characteristics of the object that most readily elicited a response when presented as dot stimuli.

Stimulus speed did not have a strong influence on orientation propensity, as long as the speeds were slow. *Servaea vestita* mostly preys on stationary insects or occasionally on ants travelling up ant trails (D.B.Z. and X.J.N., unpublished observations). Orientation propensity dropped when faster speeds, characteristic of flying animals (David, 1979; Golding et al., 2005; Boeddeker et al., 2003), were reached. Stimuli at these speeds either were not detected or were of no interest to the spider, either because they are not reachable in the case of prey or because they spell danger in the case of wasps, birds, etc., where an orientation turn could draw unwanted attention. Orientation propensity also dropped when spiders were faced with larger stimuli, which were more likely to be in the range of their predators than their prey. Stimulus contrast effects, suggested by the shape of the contrast curve, are compatible with a correlation-type model of motion detection (Hassenstein and Reichardt, 1956), which predicts that neural response magnitude varies in proportion to the square of the contrast. This line of investigation requires further research using stimuli with a wider range of low contrasts.

Spiders may be physiologically adapted to unpredictable food availability (Anderson, 1974; Greenstone and Bennett, 1978) and there have been numerous studies regarding the effect of hunger on the foraging behaviour of web-building spiders. Behavioural changes include heightened locomotory activity, risk taking, and changes in patch residence time or web morphology (Gillespie and Caraco, 1987; Uetz, 1988; Higgins, 1990; Higgins and Buskirk, 1992; Sherman, 1994). However, other studies have found that even long periods of starvation do not always cause behavioural changes in spiders (Anderson, 1974; Vollrath, 1985; Provencher and Riechert, 1991). Among spiders that do not build webs, Persons found complex interaction effects of hunger level on wolf spider patch residence time after 7 days without food (Persons, 1999). These interactions were dependent on the sensory channels through which spiders were allowed to perceive prey (visual or vibratory). Based on his observations, he suggested that reactions to sensory stimuli from prey that elicit predatory behaviour are unrelated to hunger level (Persons, 1999). However, Gardner showed that salticids, when deprived of food, increase their propensity to orient to moving tethered balls (Gardner, 1966). Our findings were similar, as we found that after a period of 7 days without food, both males and females significantly increased the overall orientation propensity toward visual stimuli. Nevertheless, while an increase in orientation propensity may raise the likelihood of locating prey, the movement it entails may make *S. vestita* more salient to potential predators. Consequently, orienting might increase the chances of being detected by the prey or, more

DISCUSSION

We found that spiders exhibited complete hunting sequences when only visual information from the AL eyes was available, and that the AL eyes mediated orientation behaviour when presented with very small, low contrast dot stimuli moving at slow and fast speeds. Taken together, this suggests that the AL eyes may be the most versatile element of the salticid modular visual system. Evidently these eyes, besides being sensitive motion detectors, also have a
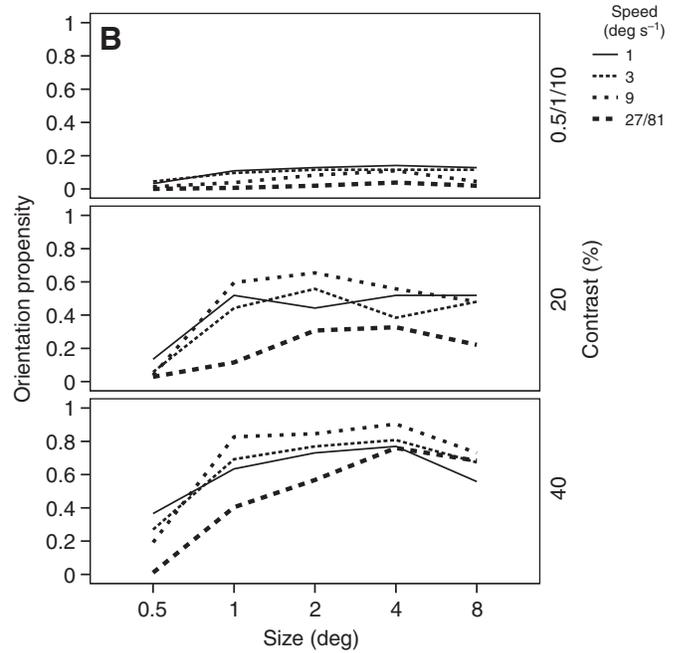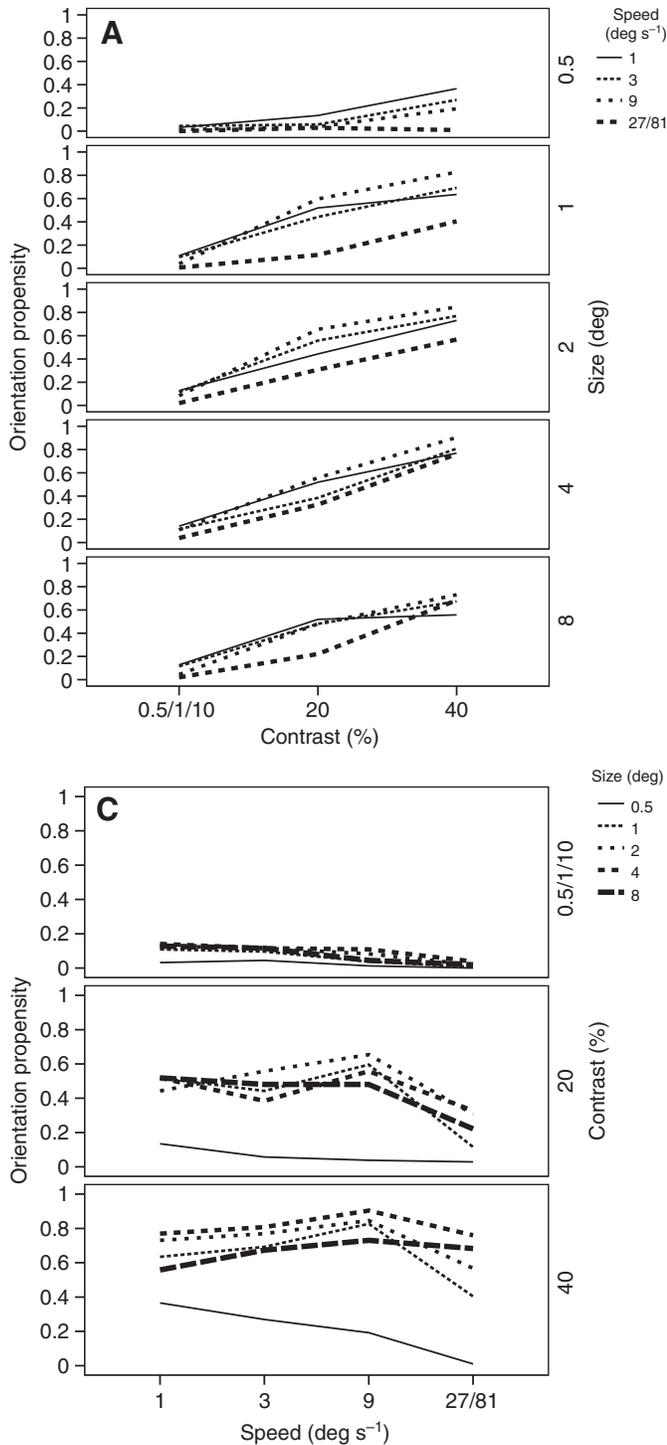
Fig. 5. Representation of three-way interaction between contrast, size and speed of dot stimuli eliciting orientation responses from spiders. A–C show the same data with different parameters on the horizontal axis (A, contrast; B, size; C, speed).

different stimulus size. Hunger level also affected the likelihood of spiders orienting toward a stimulus. After a 7 day period without food, both sexes exhibited significant increases in their orientation rate toward all stimuli. However, females increased orientation propensity when shown small stimuli more strongly than male spiders.

It is possible that the stochastic nature of prey availability is a limiting factor among sexually mature females, which may drive them to accept a wider range of prey. We found a higher orientation propensity when presenting smaller stimuli among hungry female *S. vestita* compared with sated females. This suggests that sated females may be able to afford to exhibit clearer prey-choice behaviour, as demonstrated in an earlier study on the jumping spider *Evarcha culicivora* (Nelson and Jackson, 2006). Males, on the other hand, did not show specific differences to stimuli of different sizes when sated or when hungry, other than a generalized increase in orientation behaviour.

Despite the possibility of different nutritional demands, there was no evidence of the effect of hunger on total orientation propensity differing between males and females. Both males and females showed a similar percentage increase in total orientations when not fed for a week. Furthermore, in the ramp trials, females significantly increased stalking propensity after a week of starvation, and, despite the small sample size, males also showed a similar trend. The small number of males responding in these behavioural trials is not unusual; in fact, male jumping spiders are typically not used in behavioural studies because they seem generally less motivated to complete tasks (Jackson and Hallas, 1986; Jackson and Pollard, 1996). Our results lead us to believe that this lower motivation is not due to a weaker effect of hunger on males.

Alternative explanations for higher orientation propensity in females may lie in the elaborate visual displays often made by male salticids that females evaluate during courtship (Clark and Uetz,

adversely, being located by a predator, suggesting risk assessment may affect a response seemingly as simple as an orienting 'reflex'.

Female spiders are subject to larger reproductive investment than tends to be the case for males. This, in turn, may have resulted in female spiders experiencing higher nutritional demands than males. Clear examples of this are found in lycosid spiders (Edgar, 1971) and jumping spiders (Givens, 1978). On the whole, we observed a stronger propensity to orient toward stimuli in females than males, which might be a result of higher nutritional needs. This was not expressed as a uniformly higher percentage of orientation responses towards all stimuli. Females reacted differently from males to

1992; Jackson and Pollard, 1997; Elias et al., 2006), or in possible sex-based physiological differences in the visual system of jumping spiders, as has been demonstrated in other arthropods. For example, hoverflies show sexual dimorphism in their dorsal receptive fields (Nordström et al., 2008) and male house flies have both higher spatial acuity in certain zones of the eyes and faster photoreceptor response times than females (Hornstein et al., 2000). Further work on the optics and neurophysiology of salticid visual systems is needed to investigate this possibility.

ACKNOWLEDGEMENTS

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