

## JUMPING SPIDERS ALTERNATE TURNS IN THE ABSENCE OF VISUAL CUES

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**ABSTRACT:** The abilities of four species of diurnal jumping spiders (*Helpis miniabunda*, *Portia fimbriata*, *Trite auricoma*, and *Trite planiceps*) and one species of nocturnal clubionid spider (*Clubiona cambridgei*) to maintain approximately straight paths by alternating turns in the absence of visual cues was investigated. Under infra-red light (observed using infra-red video), individual spiders were run through a maze comprising a single forced turn and then a choice of turning in the same or opposite direction to the forced turn. At the second (free) turn, each species turned in the direction opposite to the forced turn (i.e., alternated turns) more frequently than it turned in the same direction. There was no evidence that species differed in tendency to alternate turns. In nature, jumping spiders may use this ability to navigate in the absence of visual cues when foraging or escaping predators in darkness. It is suggested that alternation of turns by jumping spiders depends on proprioceptive information gathered during previous turns.

### INTRODUCTION

Turn alternation is the tendency of animals to turn in the direction opposite to the previous turn after a forced turn or at successive choice situations. This tendency has been described in a wide taxonomic range of animals (for review, see Hughes, 1989), and it has been suggested that turn alternation is used by animals in nature as a means of approximating straight paths in the absence of external directional cues (Dingle, 1965; Hughes, 1978). Maintaining straight paths may facilitate exploration, dispersal, foraging, and escape behaviours (Hughes, 1990; Richman et al., 1987).

Jumping spiders (Araneae, Salticidae) are unique amongst spiders, as they have complex eyes and acute vision (Williams & McIntyre,

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1980; Blest & Carter, 1987). Although vision-dependent orientation and navigation abilities of jumping spiders have been studied (Hill, 1979; Tarsitano & Jackson, 1992; Jackson & Wilcox, 1993), other orientation mechanisms also underlie their behaviour. For example, Land (1971) found that, following target detection by lateral eyes, jumping spiders made turns to orient toward targets and that these turns did not depend on visual feedback during the execution of the turn. That is, these turns are governed by an 'open-loop' system, whereby the turning angle is pre-set by the eyes, and the turn is mediated by internal information, rather than information received by the eyes during the turn.

Jumping spiders also retain a memory of their relative position in space, using combinations of route-referent, gravitational and visual cues. They use this information while making detours to re-orient toward targets after moving to new locations (Hill, 1979). Although Hill (1979) demonstrated that visual feedback during locomotion is not necessary for accurate re-orientation, there appears to have been no previous studies of whether jumping spiders can maintain straight paths in the absence of visual cues for pre-setting a target position. The present study investigated whether jumping spiders alternate turns, thereby compensating for deviations from straight paths, in the absence of visual cues either for pre-setting orientation or as feedback during locomotion.

## METHOD

### *Spiders*

Two species of jumping spiders, *Trite auricoma* and *T. planiceps*, and a species of nocturnal clubionid spider, *Clubiona cambridgei*, were collected in the vicinity of Christchurch, New Zealand. Another two species of jumping spider were collected from elsewhere: *Helpis minitabunda* was collected in Auckland, New Zealand, and *Portia fimbriata* was obtained from a laboratory culture originating from near Cairns, Australia. Only adult spiders with all limbs intact were used. They were maintained using the standard procedures described by Jackson and Hallas (1986).

### *Apparatus*

The testing arena was designed to present the subject with a



### *Procedure*

The spiders were maintained and tested under a laboratory photoperiod of 12L : 12D. All tests were carried out during the light phase, although no tests were conducted during the first and last 2 h of the light phase.

To begin a test, a spider was placed on the starting platform outside the light-proof cabinet. This was achieved by holding the platform in front of the spider and gently touching its hind-most legs with a camel hair brush so that it walked forward onto the platform. The spider usually stopped at the far end of the platform long enough for the test to be started. If the spider remained active, it was detained by repeatedly rotating the platform. Once the spider stopped moving, the starting platform was placed into the water (under IR light) by holding it with a hand that extended through the sleeve. The starting platform was then pushed toward the entry platform so that the two platforms joined to form a single 100-mm-long runway.

Spiders then walked off the starting platform and along the entrance platform to the 90° 'forced turn'. Half of the tested individuals of each species were forced right, and the other half were forced left. Following the single forced turn, the spider walked along the ramp until it encountered the 'choice point' where it was given the option of turning either in the same direction as the forced turn (repeating), or in the opposite direction to the forced turn (alternating). A choice was defined as having reached the end of one of the runways following the choice point. Each subject was tested once. However, if a spider failed to complete a test by leaving the arena (e.g., jumping or walking onto the water surface) or did not complete the test within 10 min, it was retested at least 2 h later. Any spiders that failed to complete the test on the second attempt were discarded.

### RESULTS

In the absence of visual cues for pre-setting a target or as feedback during locomotion, each species alternated turns more frequently than it repeated turns. The numbers of each species tested, the number and percent that alternated turns, and the result of one-sample chi-square tests can be seen in Table I. There was no evidence that the five species differed in frequency of turn alternation (test of independence,  $\chi^2 = 7.08$ ,  $df=4$ ,  $p > 0.1$ ).

**Table 1. Frequency of turn-alternation.  $\chi^2$ ; test of goodness of fit,  $H_0$ : equal proportions alternating and repeating turns.**

Species	N	Number alternating	Percent alternating	$\chi^2$	<i>p</i>
<i>Clubiona cambridgei</i>	28	24	86	14.29	<0.001
<i>Helpis minitabunda</i>	36	26	72	7.11	<0.01
<i>Portia fimbriata</i>	21	17	81	8.05	<0.005
<i>Trite auricoma</i>	79	50	63	5.58	<.025
<i>Trite planiceps</i>	60	46	77	17.07	<.001

## DISCUSSION

That *C. cambridgei* alternated turns is not surprising, as this species is a nocturnal hunter that may be heavily reliant on non-visual cues for orientation in natural conditions. Besides, turn-alternation has been previously described in another clubionid spider, *Clubiona holosericea* (Schäfer, 1982). However, that the jumping spiders alternated turns in the absence of visual cues may be more surprising. Jumping spiders are generally considered to be strictly diurnal, actively hunting during the day and seeking shelter in crevices or nests for the night (Jackson, 1979, 1988; Richman & Jackson, 1992; Wise, 1993). It is therefore interesting to find that, when visual cues are absent, jumping spiders move about on an arena rather than remaining stationary, and are able to correct for deviations from a straight path by alternating turns.

Perhaps some jumping spiders are not as strictly diurnal as is commonly supposed and may rely on non-visual orientation mechanisms during navigation and prey-capture in darkness. *Trite planiceps* is known to be able to catch flies in darkness (Forster, 1982) and there is anecdotal evidence that some jumping spiders may forage after nightfall (Reiskind, 1982). Also, many jumping spiders may be subject to attacks by nocturnal predators (Jackson, 1976; Jarman & Jackson, 1986), and these attacks may sometimes force jumping spiders to flee their nests in darkness. Once outside their nests, jumping spiders would be advantaged if they could rapidly distance themselves from the predator by approximating a straight-line escape path. Alternating turns at sequential obstructions would be a

useful mechanism for maintaining straight-line escape paths from nocturnal predators.

The present study was designed primarily to investigate only whether jumping spiders alternate turns when visual cues are absent, rather than to identify the sensory mechanisms underlying navigation in these conditions. However, because tactile cues were minimised by conducting experiments on an arena that lacked walls, it seems unlikely that turn alternation was mediated solely by tactile-dependent responses such as 'centrifugal swing and thigmotaxis' (Schneirla, 1929; see Hughes, 1989). Instead, it appears likely that proprioceptive cues were involved. Recent studies have indicated that proprioceptive feedback generated by 'bilaterally-asymmetrical leg movements' (BALM, Hughes, 1985) may be used by arthropods during turn alternation. Jumping spiders appear to rely on proprioceptive cues gathered by stepping movements of legs to mediate orientation toward visual stimuli in light (Land, 1972). That spiders also rely on proprioceptive cues to mediate turn alternation has been suggested previously by Hill (1979) and Schäfer (1982). Further studies investigating cues used by jumping spiders during orientation and navigation in darkness are clearly required.

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## REFERENCES

- Blest, A. D. & Carter, M. (1987). Morphogenesis of a tiered principal retina and the evolution of jumping spiders. *Nature*, 328, 152-155.
- Dingle, H. (1965). Turn alternation by bugs on causeways as a delayed compensatory response and the effects of varying visual inputs and length of straight path. *Animal Behaviour*, 13, 171-177.
- Forster, L. M. (1982). Non-visual prey-capture in *Trite planiceps*, a jumping spider (Araneae, Salticidae). *Journal of Arachnology*, 10, 179-183.
- Hill, D. E. (1979). Orientation by jumping spiders of the genus *Phidippus* (Araneae:

- Salticidae) during the pursuit of prey. *Behavioral Ecology and Sociobiology*, 5, 301-322.
- Hughes, R. N. (1978). Effects of blinding, antennectomy, food deprivation and simulated natural conditions on alternation in woodlice (*Porcellio scaber*). *The Journal of Biological Psychology*, 20, 35-40.
- Hughes, R. N. (1985). Mechanisms for turn alternation in woodlice (*Porcellio scaber*): The role of bilaterally asymmetrical leg movements. *Animal Learning and Behavior*, 13, 253-260.
- Hughes, R. N. (1989). Phylogenetic comparisons. In W. N. Dember & C. L. Richman (Eds.), *Spontaneous alternation behavior* (pp 39-57). New York: Springer-Verlag.
- Hughes, R. N. (1990). Mechanisms for turn alternation in the tunnelling mud crab *Helice crassa*. *New Zealand Journal of Zoology*, 17, 185-189.
- Jackson, R. R. (1976). Predation as a selection factor in the mating strategy of the jumping spider *Phidippus johnsoni* (Salticidae, Araneae). *Psyche*, 83, 243-255.
- Jackson, R. R. (1979). Nests of *Phidippus johnsoni* (Araneae, Salticidae): characteristics, pattern of occupation, and function. *Journal of Arachnology*, 7, 47-58.
- Jackson, R. R. (1988). The biology of *Jacksonoides queenslandica*, a jumping spider (Araneae: Salticidae) from Queensland: intraspecific interactions, web-invasion, predators, and prey. *New Zealand Journal of Zoology*, 15, 1-37.
- Jackson, R. R. & Hallas, S. E. A. (1986). Comparative biology of *Portia africana*, *P. albinana*, *P. fimbriata*, *P. labiata*, and *P. shultzi*, araneophagic, web-building jumping spiders (Araneae: Salticidae): utilization of webs, predatory versatility, and intraspecific interactions. *New Zealand Journal of Zoology*, 13, 423-489.
- Jackson, R. R. & Wilcox, R. S. (1993). Observations in nature of detouring behaviour by *Portia fimbriata*, a web-invading aggressive mimic jumping spider from Queensland. *Journal of Zoology, London*, 230, 135-139.
- Jarman, E. A. R. & Jackson, R. R. (1986). The biology of *Taieria erebus* (Araneae, Gnaphosidae), an araneophagic spider from New Zealand: silk utilisation and predatory behaviour. *New Zealand Journal of Zoology*, 13, 521-541.
- Land, M. F. (1971). Orientation of jumping spiders in the absence of visual feedback. *Journal of Experimental Biology*, 54, 119-139.
- Land, M. F. (1972). Stepping movements made by jumping spiders during turns mediated by the lateral eyes. *Journal of Experimental Biology*, 57, 15-40.
- Richman, C. L., Dember, W. N. & Kim, P. (1987). Spontaneous alternation behavior in animals: a review. *Current Psychological Research and Reviews*, 5, 358-391.
- Richman, D. B. & Jackson, R. R. (1992). A review of the ethology of jumping spiders (Araneae, Salticidae). *Bulletin of the British Arachnological Society*, 9, 33-37.
- Reiskind, J. (1982). Observations of night activity in *Phidippus otiosus* (Hentz). *Peckhamia*, 2, 40.
- Schäfer, M. W. (1982). Gegendrehung und winkelsinn in der orientierung verschiedener arthropoden. *Zoologische Jahrbucher. Abteilung für Allgemeine Zoologie und Physiologie der Tiere*, 86, 1-16.
- Schneirla, T. C. (1929). Learning and orientation in ants. *Comparative Psychology Monographs*, 6, 1-142.
- Tarsitano, M. S. & Jackson, R. R. (1992). Influence of prey movement on the performance of simple detours by jumping spiders. *Behaviour*, 123, 106-120.

- Williams, D. S. & McIntyre, P. (1980). The principal eyes of a jumping spider have a telephoto component. *Nature*, 288, 578-580.
- Wise, D. H. (1993). *Spiders in ecological webs*. Cambridge: Cambridge University Press.