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Prey Localization by the Waterstrider (*Gerris remigis*): Hunting Under Beacon and Non-Beacon Conditions

by

Michael R. Snyder ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Doctor of Philosophy

Department of Psychology

Edmonton, Alberta

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Faculty of Graduate Studies and Research

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled *Prey Localization by the Waterstrider (Gerris remigis): Hunting Under Beacon and Non-Beacon Conditions* submitted by Michael R. Snyder in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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Abstract

Waterstrider (Hemiptera, Gerridae) spatial representation during hunting was studied in a series of three experiments and one artificial neural network (ANN) computer simulation. In the experiments, wild-caught waterstriders were tested on tanks in controlled environments. Waterstriders were offered prey attatched to strings and lowered onto the surface of the test arena. Waterstrider hunting behaviour was videotaped and later analyzed from video playback. The experiments differed in the conditions and cues offered in the hunting situations. The first experiment examined prey capture under beacon-homing conditions. Prey was left on the water surface until the waterstrider was within 2 cm of the prey. Results show that translational and rotational movements of waterstriders were well correlated with prey location for the first and subsequent strides. The second experiment examined the significance of visual and vibratory cues produced by the prey for target localization by the hunting waterstrider. Availability of visual and vibratory cues was manipulated with opaque or transparent guillotine doors positioned just above or well below the water surface. In the absence of vibratory cues waterstriders did not initiate attacks on the prey. With vibratory cues waterstrider performance resembled control (no guillotine door present) conditions, suggesting that waterstriders can localize prey position successfully with vibratory cues alone. The ANN simulation tested rotational and translational accuracy when provided either with wavefront curvature or amplitude information. Results suggest that amplitude information might be the more likely signal used by waterstriders in hunting. The third experiment studied hunting under beacon and non-beacon conditions. Prey was placed on the water surface, then removed after the waterstrider made the first stride towards the prey. In addition, cylindrical landmarks around the outside of the testing arena were either present or absent. Statistical shape analysis of results indicates that waterstriders' strides were significantly oriented towards prey even in the absence of beacon information, although performance was better when landmarks were available. The implication is that waterstriders utilize a hierarchical strategy, relying first on beacon information. In the absence of beacon

cues, the second strategy is piloting (using landmark-based information for prey localisation) or path integration (using landmark-based information to re-calibrate locational information after each stride). Path integration without re-calibration from landmarks is a last resort.

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Chapter 1:

Research Objectives, Thesis Organization, and Background Information

Introduction

Animals move through the environment responding to a wide variety of stimuli. This locomotory responsiveness is a defining feature of animal life (Barrett, Abramoff, Kumaran & Millington, 1986). For some animals, such as certain marine polyps, the movement period is brief and largely uncontrolled, ending in a life of sessile permanency. For others, though, life is filled with locomotion, directed by a wide range of motivating factors, many apparently outside of an organism's voluntary control. Such motivated movement patterns, called tropisms, first named and studied by botanists, have been more avidly studied in a wide range of animal species, particularly insects.

Loeb (1907, 1918) was the first to systematically investigate the locomotory drives of the animal kingdom. There are many kinds of tropisms. These include geotropism (directed by gravity), phototropism (influenced by light levels), and reotropism (controlled by water current direction). Tropisms are generally viewed as "a purely physical directive reaction; that is to say, innate automatic, independent of all choice and consequently of all psychic phenomena" (Bouvier, 1922, p. 8). In modern parlance we would say that tropisms are controlled by an animal's hardwired systems.

As such, tropisms do not involve spatial representation, that is, the need for an animal to encode within its nervous system the position of important features within the environment. There was an extensive amount of early research in the field of "movement psychism" with insects. Fabre (1918, 1919), for example, carried out spatial studies with the scarab beetle *Ateuchus sacer* and the parasitic wasp *Sphex occitana*. Turner (cited in Bouvier, 1922) reported on a spider-hunting Sphegid wasp's use of what would now be termed spatial memory to move a captured prey item around numerous obstacles before reaching the nest. Ferton (1905) studied two species of solitary bees (*Osmia rufohirta* and *Osmira ferruginea*) which nest in empty shells of land snails. After moving the bees' shells from their original positions Fenton observed the search patterns the bees used to relocate their nests. As the century progressed there has been an ongoing and continual interest in how insects represent spatial information for all manner of purpose, including feeding, mating, and migration.

My research has focused on investigating the spatial representation used by hunting waterstriders (Hemiptera, Gerridae). Waterstriders, semi-aquatic insects, prey upon small arthropods that fall unto the water surface and become trapped by surface tension. The appearance of a prey item in the vicinity of a waterstrider is episodic (i.e., random in space and time) and punctate (i.e., of very short duration). A waterstrider will generally respond to the detection of a prey item by orienting towards it and moving to intercept. If the prey item disappears (e.g., flies away) after it is detected, a waterstrider may initiate a search to try and locate the prey.

Broadly speaking, my research interests include behaviour, spatial representation, predation, simple nervous systems coping with complex environments, and modularity of systems. Waterstriders represent an ideal system to study these topics. To begin with, my study of waterstriders is behavioural in nature. More specifically, it involves the investigation of hunting behaviour. The representation of spatial information in general is a compelling field of study. Animals are constantly making spatial representations of one type or another, but spatial representation during hunting is an especially interesting approach to the topic for a variety of reasons.

Although there has been a recent surge of interest in many areas of spatial representation (e.g., Healy 1998; Wehner, Lehrer, & Harvey, 1996), little research has focused on spatial representation in predation. Admittedly, within a broad contextual framework it is acceptable to define most acts of foraging as predation, such as pigeons identifying preferred pieces of grain from unappetizing distracters (e.g., Reid & Shettleworth, 1992), although practically speaking this is not what is generally thought of as a predatory event. One of the advantages in studying predatory behaviour in insects is that it is possible to do so under relatively controlled laboratory condition (in contrast, imagine bringing a cheetah into the laboratory to study its ability to capture an antelope). Even within the well studied field of spatial representation, navigation, and target localization in arthropods there has been a surprising dearth of studies relating to spatial representation during predation. Some exceptions include work with beetle and dragonfly larvae (e.g., Banks, 1957; Dixon, 1959; Etienne, 1972; Laing, 1937; Sandness & McMurthy, 1972), mantids (Mittelstaedt, 1957), jumping spiders (e.g., Jackson & Pollard, 1996; Jackson & Wilcox, 1994, 1998), and scorpions (Brownell, 1984).

Additionally, predatory attacks are rapid events. Unlike a bee or pigeon searching for its nest or for a food site, one may argue that spatial representation during a predatory attack need be cognitively streamlined to reduce the processing load. Spatial representation during an attack includes the added complexity of processing relevant information in very short time periods. Furthermore, as pointed out by Rilling, Mittelstaedt, and Roeder (1959), prey capture behaviour is quite complex, involving a greater number of and variation in inputs than many other behaviours. Admittedly, nervous systems have evolved the ability to process quantities of information rapidly. However, for small nervous systems, such as those of insects, there is not a large resource available. Consideration of such issues are related to my interest in simple nervous systems coping with complex environments. The hunting behaviour of waterstriders offers interesting opportunities to examine some of these questions.

There is also the issue of nervous system modularity. I am not especially interested in the specifics of the neurology of insect (or other animal) brains. Rather, I am more interested in the functional organization of the system I am studying as a whole. This is another reason why I find insect studies of behaviour fascinating. Although insects have relatively small brains, they perform an impressive array of complex behavioural feats, analogous to much of the behavioural repertoire of vertebrates (Menzel, 1983). Braitenberg's (1984) synthetic approach to the nervous system, and more broadly to behaviour, suggests to me that modularity of neural and behavioural systems provide insects with the ability to cope effectively with the complexities of their environment despite small central nervous systems (CNSs).

Thesis Organization

The thesis is organized as a collection of papers. That is, separate chapters of the thesis are intended as reports for publication. Hence, the reader will encounter some redundancies in the introductory sections of the separate chapters. In addition, some of the overriding themes for this series of studies are laid out in the introduction to the thesis. The current chapter introduces and discusses general issues of navigation and spatial representation and provides a review of the relevant studies involving waterstriders pertinent to my research. The second through fourth chapters cover three experiments investigating spatial representation by hunting waterstriders, with the final chapter offering summarizing and concluding comments.

The research presented in chapters two to four forms a progression in the complexity of spatial representation involved in representing the position of a prey item by waterstriders. Chapter two explores waterstriders' ability to accurately localize, in terms of direction and distance, a prey item that is present on the water surface. Adult waterstriders (*Gerris remigis*) were given access to live prey items (ants, *Formica* spp.). In response to stimuli produced by prey items dropped onto the water surface at various distances and angles, waterstriders move towards the prey in a series of "strides". The rotational and translational components of a stride enable a hunting waterstrider to match the angular deviations and linear separation between itself and a prey item. I report on strategies used by hunting waterstriders to locate and respond to the presence of live prey. This study involves beacon homing conditions, that is, situations in which stimuli produced by the prey serve to guide a waterstrider's movements.

Chapter three addresses the question of whether or not visual feedback from the prey item is needed for waterstriders to successfully localize the prey's position. Adult waterstriders (*Gerris remigis*) were tested in a behavioural study to determine the importance of visual and vibratory stimuli provided by their prey (ants, *Formica* spp.). Individual waterstriders were placed on one side of an arena and a prey item on the other, separated by a guillotine barrier. Using transparent or opaque barriers positioned above or below the water, four visual and vibratory stimuli conditions were available to the waterstriders: visual and vibratory stimuli, vibratory but no visual stimuli, visual but no vibratory stimuli, or no visual or vibratory stimuli. Waterstriders only initiated attacks on prey when they received vibratory stimuli; the presence or absence of visual cues did not affect rotational or translational movements of the waterstriders towards the prey during an attack. Given that vibratory cues appear to direct waterstrider attacks under beacon homing conditions, two methods for representing the position of the prey using surface wave information are proposed. An artificial neural network (ANN) simulation suggests that a wave front's amplitude, rather than its curvature, provides more useful information for a waterstrider localizing a prey item's position.

In chapter four the focus of the research shifts from instances of beacon homing to non-beacon homing. In a semi-naturalistic testing arena, waterstriders (*Gerris remigis*) were provided with prey items (houseflies, *Musca domestica*). Immediately after the initiation of an attack by a waterstrider the prey was removed from the water surface. Trials were conducted under two environmental conditions, landmarks absent and landmarks present. The movement patterns of waterstriders were interpreted using statistical shape analysis (SSA) to determine if they could continue to accurately represent the position the prey after its removal from the water surface. Results indicate that waterstriders do spatially represent the prey position and are able to continue their attack on prey under non-beacon homing conditions. Further, waterstriders overshoot the prey target position by less and are more directed towards the target position when landmarks are available, suggesting that landmarks are significant in forming an accurate spatial representation. However, even in the absence of landmarks waterstriders will continue to move in the general vicinity of the target position, implying that a hierarchy of navigational techniques (e.g., beacon cues, piloting, path integration) are employed during hunting.

The final chapter provides summarizing comments and discussion of this phase of my research program. Conclusions about the importance of this work in relation to the broader field of spatial representation in insects and other animals are offered. Additional comments on a future program of study are also provided.

Why Waterstriders?

There are a number of reasons for selecting waterstriders to study insect spatial representation. First, they exist in a two-dimensional world, confined to the surface layer of streams and ponds.[1] The vast majority of a waterstrider's interactions when hunting for food, identifying mates, or defending territory are confined to the upper plane of the water surface. The lack of a third dimension greatly reduces the complexity of constructing and analyzing models of their spatial representations. Second, waterstriders are predators for whom the appearance of their prey is episodic and punctate. This requires waterstriders to react rapidly to the presence of a prey item if they are to capture it. Waterstriders' relatively small central nervous system (according to Guthrie, 1961, some 400,000 neurons) is a third reason for working with them. This is an especially interesting point when considered in relation to the need for rapid responses in hunting: waterstriders have relatively little cognitive processing power at their disposal. Their hunting behaviours are moderately complicated and quite successful, but must be executed with limited neural resources.

An additional point is that waterstriders are not central place foragers like the social insects (i.e., bees, ants, wasps, and termites) on which the vast majority of insect navigation and spatial representation work has been carried out. Central place foragers leave from and

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[1] This is not strictly true. Some waterstrider morphs can fly, females can pull themselves through the water surface to lay eggs on submerged plants or rocks, and waterstriders will sometimes thrust their prothoracic legs below the water in an attempt to capture submerged prey. In addition, waterstrider eyes are constructed to look for predators approaching from above or below. However, with respect to most hunting behaviour, waterstriders are generally restricted to the flat surface of the water.

return to the same place, usually a nest, when searching for food. In contrast, waterstriders do not have a fixed place in the environment from which they initiate and conclude attacks on prey items. Comparing how waterstriders and central place foragers represent spatial information is an interesting venture. Similarities would suggest underlying consistencies in behavioural, neuronal, and/or environmental features that are involved in spatial representation across insects (and possibly other arthropods). Likewise, differences between waterstrider and central place foraging insects could have implications for the different needs and drives at work between the social and non-social insects. Finally, there is a substantial literature base dealing with waterstriders, although very little of it relates to spatial representation, and none directly to issues of behavioural mechanisms involved in spatial representation during hunting.

Background: Navigation and Spatial Representation

Navigating animals (where navigation is defined as the process of determining and maintaining a course from one place to another) have three techniques available to them: beacon homing, path integration, and piloting. All involve forming spatial representations, although the information encoded varies with each technique. With beacon homing an animal orients itself with respect to a detectable target which, using a feedback system, guides its path toward (or away from) the beacon/target. Path integration, or dead reckoning as it is also termed, is the process of integrating velocity with respect to time. Path integrating animals represent a target location as a vector between themselves and the target, continuously updating the vector as they move. Piloting involves plotting a path using environmental features (i.e., landmarks) and a map (internal or external) that identifies geometric relations between perceived features and the target. Animals using piloting may represent locations in a variety of ways, but all involve the use of one or more landmarks. Gallistel (1990, p. 58) maintained that within the interplay between path integration and piloting, path integration provides mobile animals with the underlying information about their position in the world. Even in familiar environments, path integration is an animal's primary means of determining position, only occasionally using piloting to take a positional "fix".

The information used to determine course heading using path integration differs slightly depending on whether the distance traveled is short or long. For short distances inertial path integration is feasible. Inertial path integration requires no information about the environment that the animal travels through; all directional and distance information is determined from non-visual stimuli (e.g., proprioceptive, kinesthetic, and vestibular information). Some arthropods, such as spiders (Görner, 1973, cited in Wehner, 1984; Mittelstaedt, 1974, cited in Wehner, 1984), crabs (Herrnkind, 1972, cited in Wehner 1984), and isopods (Hamner, Smyth, & Mulford, 1968), have been shown to use this form of path integration. Over longer distances and/or complex routes, however, inertial path integration accumulates errors, which can result in an animal traveling significantly off course. In this case animals require an environmental directional reference point. Celestial bodies are particularly good directional references. A variety of animals, including *Aplysia* (Hamilton & Russell, 1982), bees (Dyer & Dickinson, 1994; Gould, 1980, 1984), and pigeons (Phillips & Waldvogel, 1988) use the sun, while others, such as indigo buntings (Emlen, 1967a, 1967b) and garden warblers (Wiltschko, Daum, Fergenbauer-Kimmel, & Wiltschko, 1987), use star patterns to determine a directional reference point.

Navigation by piloting requires the use of stable points of reference (i.e., landmarks) in the environment. In piloting, an animal must determine its position and heading in the environment. Position is represented in a coordinate system that is anchored to a map (either internal or external) while heading is the animal's orientation on the map. Animals make use of the sun, moon, stars, and various earth-bound features (e.g., vegetation, rocks, etc.) to determine their heading (Gallistel, 1990). Positional information can be derived from taking various forms of fixes, or sightings, on objects that occupy a known place on the map. There are a number of ways of taking positional fixes, including the use of lines of sight, arcs, and circles of position, as well as stationary and running fixes (Gallistel, 1990). Animals can also use global determination of position and heading. Global fixes do not require the identification of individual points of reference in the environment. Rather, the overall configuration of points is used. The issue becomes one of image alignment. Global fixes are obtained by comparing anticipated and actual perceived images. The anticipated image comes from the animal's internal map and/or path integration representation of its position. The animal can use any discrepancy between the anticipated and actual images to determine its position and heading. Global fixes, also described as "snapshot" navigation in the insect literature, have been proposed as a mechanism by which insects including hoverflies (Collett & Land, 1985), ants (Hölldobler, 1980), and honeybees (Cartwright & Collett, 1983, 1987) can return to a specific position in space.

Much of the research into navigational processes and spatial representations, especially in insects, lends support to Gallistel's claim of the importance of path integration as the primary formulating mechanism of spatial representations. Copious studies into navigation by ants and bees show that path integration holds an important place in these insects' ability to find their way back to their nest after locating a patch of food (e.g., Kirchner & Braun, 1994; Müller & Wehner, 1988; Wehner, 1987; Wehner & Srinivasan, 1981). The environment of these insects include spatial features that are relatively consistent and non-ephemeral, thereby allowing the use of landmarks for navigational purposes (e.g., Collett, 1992; Collett, Dillmann, Gieger & Wehner, 1992; Hölldobler, 1980; Lehrer & Collett, 1994; Schmidt, Collett, Dillier, & Wehner, 1992). In addition, ants and bees, which are central place foragers, navigate to and from stable targets (e.g., nest sites, foraging patches). This stability provides ample opportunity for the insects to learn the features of useful landmarks (e.g., Gould, 1985; Lehrer, 1996; Zeil, Kelber & Voss, 1996). In contrast, episodic and punctate events, often found in predator-prey and some mating situations (e.g., Brownell, 1984; Mast, 1912; Mittelstaedt, 1957), have not been extensively studied to determine how targets are integrated into an animal's representation of the environment. In contrast to wasps' ability, for example, to learn the position of their nest opening relative to landmarks (e.g., Zeil, 1993a, 1993b), the transitory nature of the target in hunting situations does not allow the predator the leisure to learn the target's position relative to surrounding landmarks. Instead, the target must be rapidly placed within a spatial representation that the animal can use for navigation.

Background: Waterstriders

Waterstriders (Hemiptera) are semi-aquatic insects that inhabit the surface of ponds and streams. They are active predators and opportunistic scavengers that locate their prey and social partners by surface vibrations (Murphey, 1971b) and visual cues (Liche, 1936, cited in Dahmen, 1991; Spence & Wilcox, 1986). Over the last 15-20 years, waterstrider behaviour has been studied primarily within an ecological framework, where the focus of interest is the fitness consequences of behaviours with respect to reproduction and survival. Within this methodological approach, issues of social hierarchy (e.g., Rubenstein, 1984), communication patterns (e.g., Jablonski & Wilcox, 1996; Wilcox & Spence, 1986), mate competition (e.g., Spence & Wilcox, 1986; Wilcox, 1984), and territoriality (e.g., Wilcox & Ruckdeschel, 1982) have been studied.

Murphey (1971a, 1971b) demonstrated that waterstriders possess water surface vibration receptors in the tibial-tarsal joints of their six legs and that they use these receptors to calculate the initial rotation necessary to match the angular deviation between themselves and their prey. Similar vibration receptors, which fulfill the same function, have been found in other arthropods (e.g., Brownell, 1984; Murphey & Mendenhall, 1973). Water surface vibrations provide waterstriders with a significant amount of information about their environment. Similarly, waterstriders engage in intraspecific communication through the generation of high frequency ripple signals (Jabonski & Wilcox, 1996; Wilcox, 1972; Wilcox, 1979; Wilcox & Di Stefano, 1991; Wilcox & Spence, 1986).

In addition to a system that responds to surface wave vibrations, waterstriders also possess a visual system known to play an important role in a number of behaviours. More than 85% of the neurons in the *Gerris* CNS are located in the optic lobes (Guthrie, 1961). Most research into the waterstrider visual system has focused on its role in drift compensation. Because waterstriders move in discrete increments, or "strides", using their middle two legs to provide thrusting strokes, they cannot maintain a fixed position in a current. By way of analogy, waterstriders move like a rowboat with two oars (see Bowden, 1978a, 1978b for the mechanics of waterstrider locomotion). To maintain a relatively constant location on a stream, waterstriders identify a landmark on the shore and when the current pushes them past this landmark they stride forward and subsequently drift back again (Fairbairn & Brassard, 1988; Junger & Varjú, 1990). The ommatidia (the subunits into which the insect compound eye is divided) of the dorsal, middle, and ventral regions of the eye actually respond slightly differently to polarized light due to differences in their ultrastructure (Bohn & Täuber, 1971).[2] It is believed that these differences help contribute to the greater resolution and sensitivity of the visual streak.

Drift compensation has implications for the defense of mating territory by males, but has been most studied with respect to food territoriality. The fastest flowing portion of a stream is the most food productive; waterstriders vie for and defend lead positions producing a feeding hierarchy (e.g., Rubenstein, 1984). Less dominant waterstriders in the social hierarchy will defend other territories, including side ponds, in a similar manner (e.g., Blackenhorn, 1991). Essential to this procedure is an ability to compensate for drift. Junger and Dahmen (1986) indicate that it is the dorsal ommatidia of the waterstriders' eyes that are most significant in visually mediated drift compensation. Junger and Varjú (1990) ruled

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[2] It is not clear what significance the detection of polarized light is to waterstriders. Due to the structure of the arthropod compound eye most insects are readily capable of detecting polarized light. Unlike vertebrates, in insects the photoreceptor membranes of the eye are compressed into narrow tubes, called microvilli. As a result of this anatomical development the visual pigment rhodopsin is aligned along the long axes of the microvilli. The effect is maximal absorption of polarized light when the axis of polarization coincides with that of the microvilli (Wehner, 1976). In insects like bees and ants the specialization of the compound eyes as polarized light detectors plays a crucial role in long distance navigation (e.g., Gould, 1980; Müller & Wehner, 1988)

out the use of air current detection and tactile perception of water currents in drift compensation, concluding that the only the visual system is utilized for this function. Junger (1991) elaborated on this research, demonstrating that waterstriders utilize a discontinuously working position servo in drift compensation. In practice, this would require a waterstrider to select a distinctive stationary landmark to measure its displacement from. When a waterstrider drifts too far away from the landmark it executes one or more strides to move it back to its previous location. How, exactly, a waterstrider selects a specific landmark is unknown. Junger (1991) indicated that only objects relatively close to the waterstrider would generate sufficient image displacement that could serve as suitable input for the position control system and speculates that waterstriders possess a memory for landmark constellations as do other insects (e.g., Cartwright & Collett, 1982, 1983; Collett & Land, 1985).

In the course of research into the drift compensation mechanism it has also been shown that each compound eye possesses 920 ommatidia arranged in approximately 40 horizontal rows. 30% of the ommatidia look up, 30% look down, and the remaining 40% are arranged in a visual streak of high resolution directed at an area within ±5° of the horizon (Dahmen & Junger, 1988). Dahmen (1991) determined that there is a pronounced visual streak along the equator of the eye and a forward binocular overlap of less than 10° below the equator of the eye, increasing to 10° at the equator, and 20° above the equator. The visual streak contains overlapping vertical deep pseudopupils and appears to be dedicated to the perception of objects on the horizon. The vertical sampling interval increases from 0.55° in the front to 2.5° in the back, and the horizontal sampling interval goes from 2.0° in the front to 2.5° in the back. This implies that the waterstrider eye has evolved to monitor the vertical position of objects at the expense of visual resolution. Above (up to 45°) and below (down to -20°) the visual equator Dahmen (1991) proposed that the eye is adapted to perceiving constant relative height or depth. Finally, the dorsal portions of the eyes show a 10-20° binocular overlap in the forward direction (Dahmen, 1991).

In Murphey's (1971b) experiments vibratory receptors were lesioned. Although prey items should have been visible (they were less than 10 cm from the waterstrider), waterstriders still made incorrect orienting rotations towards the prey, demonstrating the significance of vibratory stimuli in localizing the target. Wilcox (1979) blinded male waterstriders, showing that vibratory communication signals provided sufficient information for the males to correctly identify females and mate with them. These results, combined with the relatively poor visual resolution of the waterstrider eye for small objects, suggest that while visual cues might play some role in hunting live prey, waterstriders rely primarily on vibratory information to locate their prey.

To my knowledge no one has studied issues of navigation or spatial representation in waterstriders directly, but there are several papers detailing the presence of territoriality in waterstriders. These papers did not describe how waterstriders define and represent their territorial boundaries, but rather with the evolutionary advantage conferred by establishing a territory. Briefly, waterstriders establish territories for foraging (e.g., Jablonski & Wilcox, 1996; Vepsäläinen & Nummelin, 1985a; Wilcox & Di Stefano, 1991; Wilcox & Ruckdeschel, 1982), or mating purposes (e.g., Hayashi, 1985; Vepsäläinen & Nummelin, 1985b), or both (e.g., Blanckenhorn, 1991; Rubenstein, 1984).

Wilcox and Ruckdeschel (1982) found that when deprived of food, *Gerris remigis* late instars (i.e., late juveniles) and adults of both sexes establish and defend small territories, driving intruders away. Although the features used by waterstriders to define a territory were not established, the researchers did note that territories were usually set up in easily defended areas, often bounded on two or three sides by rocks. This suggests that territories are not selected at random, but are chosen based on the presence or absence of identifiable, desirable features. Vepsäläinen and Nummelin (1985a) determined that females of the species *Gerris najas* and *Gerris cinereus* also hold territories for foraging purposes. Because food drifts downstream along distinct paths, the current establishes patches of high and low food resource levels. These waterstriders established short-term territories in highly productive stream patches, driving intruders away. Site fidelity was probably maintained by a mechanism similar to that seen in drift compensation, although the researchers investigated no specific landmark features.

Male *Gerris elongatus* establish mating territories when they discover a good ovaposition (egg-laying) site (Hayashi, 1985). Once a male positions himself within a territory he emits high frequency calling signals to attract females. When a female approaches, the male switches to courtship signals and, if she is receptive, leads her back to the ovaposition site. Leaving a location and subsequently guiding another waterstrider back to it implies that the male may represent the ovaposition site in memory. Unfortunately, Hayashi was not interested in this aspect of the territorial behaviour and failed to mention how far away from the ovaposition site a male would travel before returning. More suggestive of the presence of strong spatial representations of locations on a pond is Vepsäläinen and Nummelin's (1985b) study of mating territories in male *Limnoporus rufoscutellatus* waterstriders. The males usually float anchored by one foot to a fixed object, treating it as the centre of an approximately 50 cm diameter territory. Territories were identified by site fidelity and aggressive behaviour towards intruders. Vepsäläinen and Nummelin found that males would return to their territories after leaving them. In one laboratory test the arena was shaken violently, driving males out of their territories. All of the males subsequently returned to their territories when the vibrations subsided. In another treatment food was only provided at a "restaurant". Males would leave their territory, go to the restaurant, capture prey, and either eat the prey there or take it back with them when they returned to their territory. Under natural conditions males were also observed to leave their territories to patrol the circumference of the small pond for some minutes before returning to the centre of their territories.

Taken together, these examples provide strong support for the hypothesis that waterstriders of various species are capable of representing spatial locations in memory. The work of Vepsäläinen and Nummelin (1985b), in particular, suggests that waterstriders can remember spatial information for at least limited periods of time and can use this information to return to fixed positions in space from a variety of directions. Path integration, piloting, or some combination of the two could account for the territorial behaviours described in the literature.

There are three sensory systems that appear to be most important to waterstriders. These are the visual, vibration detection, and olfactory systems. There is a large body of research concerning the visual systems of insects, in general, and a relatively detailed account of the visual system of waterstriders, in particular. While it is commonly conceded that the vibratory detection system is extremely significant for waterstriders' life on the water surface, only a moderate amount of detailed research has been directed at this sensory system. With respect to the olfactory system, aside from a vague consideration that waterstriders may use this sense for some specific, and largely undefined, tasks, little is known about this system. Junger (1991) has demonstrated that olfactory cues do not play a role in laboratory tests of drift compensation.

There is some debate over what role the visual system plays in waterstrider behaviour. Certainly their visual system must be important for waterstriders given the substantial weighting given to the optic lobes within the CNS. It is known that the visual system is necessary for waterstriders to maintain their position on a moving body of water. Waterstriders also use visual cues to avoid predation. However, the degree to which vision is used for predation or mate selection has not been fully determined.

Besides drift compensation waterstriders certainly use their visual system to avoid falling prey to other animals. Anyone who has worked with waterstriders can testify to the difficulty of catching them; waterstriders can detect the presence of a stalking ethologist when he is two meters away on the shore. Although not directed at the issue of predation, Junger's (1991) experiments demonstrate that waterstriders can utilize landmarks at least 100 cm distant. However, beyond this there appear to be no formal studies of the importance the waterstrider visual system in the dection of predators or other threats.

It has been suggested that waterstriders use their visual system to some degree during predation (e.g., Jamieson & Scudder, 1979). Some species of waterstriders have the visual acuity necessary to detect some relatively small objects at a distance (e.g., Junger, 1991; Junger & Varjú, 1990). In addition, waterstriders feed opportunistically on carrion found on the water surface. Since already dead prey do not produce vibrations it stands to reason that waterstriders locate these food items visually, although A. Tyre (personal communication, May 1993) suggests that olfaction may play a role in locating carrion. Personal observations with *Gerris remigis* suggest that detection of carrion is different from that of live prey. During the course of the study detailed in chapter four, dead crickets were offered to waterstriders after the daily experimental trials with live prey were completed. Waterstriders often passed within 2 cm of a cricket, apparently without recognizing it as food. Similarly, although positioned close to a dead cricket a waterstrider could be easily lured away from this ready food source by the presentation of a live prey item (a housefly) 15 or 20 cm away on the water surface. Unfortunately, no formal studies have been conducted that directly test the role of the visual system in identifying or capturing prey items during active predation.

Based on several experiments not examining predation, it seems likely that there is a species-dependent factor in the use of the visual system in prey capture. Spence and Wilcox (1986) examined the mating system of two species of waterstriders. They found that *Limnoporus dissortis* males are unable to determine the sex of other waterstriders visually and depend entirely upon the detection of repel ripple signal vibrations generated by other males for identifying the sex of another waterstrider.[3] When an *Limnoporus dissortis* male approaches another waterstrider, if no repel signal is produced the male proceeds with mating behaviour. *Limnoporus notabilis* males, however, appear at least partially capable of using visual cues to determine the sex of another waterstrider. *Limnoporus dissortis* and

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[3] In many species of waterstriders males can produce a series of high frequency surface vibrations. These vibrations are used to warn other males away from defended territory, to locate mates, and in determining social hierarchy (e.g., Jablonski & Wilcox, 1996; Wilcox, 1972, 1979).

Limnoporus notabilis are closely related hybridizing species. The fact that they show differences in the use (or acuity) of their visual system suggests that the use of vision in predation could be highly dependent upon the species selected.

Waterstriders have vibration receptors located in the tibial-tarsal joints of all six legs, similar to receptors found in other arthropods (e.g., Brownell, 1984; Murphey & Mendenhall, 1973). Murphey (1971b) demonstrated that these vibration receptors are used to detect the position of prey. When a waterstrider detects the surface vibrations produced by a small insect that has fallen onto the water and is struggling to escape the surface tension, the waterstrider will rotate so that it is oriented towards the prey. Murphey (1971a, 1971b) performed a series of laboratory experiments in which he lesioned various combinations of vibration receptors to study this initial rotational response of the waterstrider to prey. These studies demonstrate that the vibration detection system provides waterstriders with highly accurate information about the direction of the prey. Murphey (1971b) speculated that the amplitude of surface vibrations provide waterstriders with information about the distance to the prey item.

Murphey's experiments indicate that waterstriders can detect prey from any direction. Jamieson and Scudder (1979), however, demonstrate that a waterstrider shows a marked preference for attacking prey no more than 100° to the right or left of its longitudinal body line. This is likely due to the additional stroke of the mesothoracic (i.e., middle) leg required to rotate the waterstrider more than about 100° (Murphey, 1971a); the additional stroke may require time during an attack which the prey item can make use of to escape.[4] Despite this knowledge, relatively little is known about the actual vibration receptors. Through lesioning experiments, Murphey (1971b) showed that the primary vibration receptors are located in the tibial-tarsal joint, although he suggests that there may be additional receptors located at other leg joints. The existence of these secondary

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[4] By way of analogy, think of a waterstrider as a small rowboat with two oars. To turn left, stroke with the right oar, and vise versa. To rotate through an especially large turn more than one stroke with the same oar may be required. To move forward, stroke with both oars together.

receptors has not been confirmed or denied. It is also not known if the vibration receptor in the tibial-tarsal joints are directionally sensitive. Murphey's (1971b) model of waterstrider prey detection assumes that the vibration detectors are non-directional, although some of his data suggest that the receptors may be directionally sensitive to a very limited degree. Snyder's (1998) artificial neural network simulation that modeled the orienting behaviour of waterstriders towards prey operated on the assumption that the receptors were non-directional. No controlled studies have been carried out to address this question. In addition, as mentioned above, it is not known to what degree the waterstriders' visual and vibration detection systems interact in predation.

There is no direct information on the neuronal control system involved in prey detection via the vibratory system. However, based on his observation that motor neurons that are synchronized during certain movements produce parallel firing rate changes, Murphey (1971b) has suggested that

> in some way interneurons receive and analyze the information concerning the direction of a source of ripples and the activity in this group of interneurons then releases a coordinated motor response appropriate to the pattern of the sensory input. (p. 183)

Similarly, because a vibration produced directly behind a waterstrider results in a large rotation either to the right or to the left (by a stroke from the left or right mesothoracic leg, respectively), rather than a forward movement (by both right and left mesothoracic legs stroking together), Murphey inferred that somewhere in the CNS there are inhibitory interactions between receptors.

Besides predation, waterstriders use their vibration receptor system for detecting and interpreting ripple signal communications. Male waterstriders produce a variety of different high frequency ripple signals. As already indicated, these signals can be used to attract sexually receptive females (Wilcox, 1972), to distinguish the sex of a waterstrider (Wilcox, 1979; Wilcox & Spence, 1986; Spence & Wilcox, 1986), and to identify and defend territories (Hayashi, 1985). Besides the fact that waterstriders produce and utilize ripple signals for communication purposes, little is known about how they actually detect, identify, and interpret such signals, or even the location of the vibration receptors involved in ripple signal communication.

Research Questions

The underlying goal motivating my research is to determine how waterstriders spatially represent the position of prey during hunting. There are a variety of questions and issues that derive from this goal. In studying waterstrider spatial representation, orientation and locomotion are observed and analyzed. A central factor involved in this process involves distinguishing between random and non-random movement. Truly random movement by a waterstrider with respect to a prey item would suggest that there is no spatial representation of the target's location. Under beacon homing conditions, such as those described in chapters two and three, it would seem, on the surface, to be a relatively straightforward matter to identify random movements; any movement away from the prey item could qualify. Of course, there could be a problem with such a definition. Movement away from the prey might not, in fact, be random; it could, actually, be directed (e.g., Kareiva & Shigesada, 1983). However, this would result in a non-productive hunting behaviour. As it is unlikely that waterstriders easily confuse prey stimuli with cues indicating a potential predator, defining movement away from the prey as non-predatory is not a great concern. Nevertheless, this does raise the issue of the effectiveness of using categorical descriptions based on directional movements as indicative of random or non-random locomotion.

In the two beacon homing studies (chapters two and three), because there is a clearly defined target (i.e., the prey item) which is continuously available to the waterstrider, movements directed towards the beacon are considered to meet the requirements of non-random movement. Similarly, as the same beacon is available across multiple strides, the data can be consistently interpreted as to whether or not a waterstrider's movement takes it closer to the prey. The data analysis applied to these studies is quite traditional in its use of rotational errors and distance moved compared to the remaining distance to the target.

However, in the non-beacon homing study (chapter four) this sort of simplistic behavioural definition of non-random movement and the associated method of data analysis is not sufficient. Because there is no longer a physical target in the non-beacon situation, it seems necessary to move towards a more quantifiable interpretation of what is, or is not, movement directed towards a particular place in space. Issues of randomness become more significant.

Various stochastic models of random movement could be applied to this question. Generalized models of random walk (e.g., Bovet & Benhamou 1988; Siniff & Jessen, 1968; Skellam, 1951) or models specific to insect movement (e.g., Jones, 1977; Kaiser, 1976; Kareiva & Shigesada, 1983; Turchin, 1991) could be used to determine random and non-random movement in waterstrider hunting. In many respects waterstriders are ideally suited to the application of random walk models. In most situations animals do not travel in discrete, quantifiable legs of a journey. Rather, the path must be somewhat arbitrarily divided into lengths based on travel times or distances. Waterstriders, however, move in a series of strides. As such, the strides provide the discrete path lengths required for random walk models.

There are, however, other methods that can be applied for the identification of random and non-random patterns. These involve treating positions of predator and prey as the identifying points on a shape, or pattern, for analysis. Traditionally, when dealing with shape-related information, biologists have often made use of techniques termed "multivariate morphometrics", that is, the use of ratios of distance to angles, or the use of distances or angles in isolation for comparative purposes. Allometry, differences in shapes associated with size, is another often-used approach. Statistical shape analysis (SSA), which I have opted to use, provides another technique. SSA works with the complete geometric object rather than with quantities derived from the object (Dryden & Mardia, 1998).

SSA has been used for a number of purposes, including archeology (Broadbent, 1980; Kendall & Kendall, 1980), image analysis (Anderson, 1997 cited in Dryden & Mardia, 1998) and astronomy (Edmunds & George, 1981). Biological applications have typically dealt with differences in morphological shapes. Examples include examining shape differences in mouse vertebrae (Mardia & Dryden, 1989), gorilla skulls (O'Higgins & Dryden, 1993), and MRI brain scans of schizophrenic and normal patients (Bookstein, 1996). However, to the best of our knowledge, SSA has not previously been applied to questions involving the movement patterns of animals, although it is ideally suited for such analysis. A more extensive description of the theory and methodology of SSA can be found in chapter four.

My research involves questions of what features in the environment are used by waterstriders for representing the spatial position of their prey. In the two beacon homing studies the seemingly obvious guiding feature is the prey itself. What is it about the prey, though, that waterstriders use in determining its location? The first study demonstrates that waterstriders are very adept at reaching their prey's location. Waterstriders orient and move in such a way as to rapidly minimize the distance between themselves and their targets. Results from this study indicate that waterstriders are not simply guided towards prey through some form of tropic response, but that their nervous systems process sensory information to provide estimates of prey location with respect to their own positions (i.e., in egocentric coordinates). The second study shows that of the sensory information available to waterstriders, it is surface wave vibrations produced by the prey rather than visual cues that are most important in fixing prey location in a spatial frame of reference.

Under non-beacon homing conditions (chapter four) the question of what features were utilized in spatial representation become less obvious. Behaviourally, there was also the issue of whether or not waterstriders would continue an attack on a prey item in the absence of feedback from the target. As experimental trials demonstrated, waterstriders continue attacks initiated under beacon homing conditions even after the beacon source is removed. Additional observations indicate that waterstriders will sometimes execute what appear to be extensive searches for missing prey. Therefore, the question becomes one of how waterstriders represent the location of an object that is not providing reference cues about its position? As discussed, two techniques available to animals involve path integration or piloting. Based on waterstriders' well developed visual system it was anticipated that they would make use of landmarks, as they do in drift compensation, to represent the location of the target. Analysis of movement patterns under landmark absent and landmark present conditions shows that waterstriders overshoot targets in distance less and are more directed towards targets when landmarks are available. This implies that waterstriders make use of landmarks to represent the position of prey items.

Chapter 2:

Rotational and Translational Accuracy of Hunting Waterstriders Under Beacon Homing Conditions

Introduction

The most basic form of guided navigation involves orientation by moving towards (or away from) an object fixed at one position in space, designated as beacon homing. Beacons can take a variety of forms; all that is required is that the beacon is salient to the organism and provides a constant reference point to direct locomotion. A classic human example is the use of channel lights to guide ships between rocks and into a harbor at night. Beacon homing is a standard navigational technique employed by a wide range of organisms. *Aplysia* guides its swimming by the position of the sun (Hamilton & Russell, 1982), ants select salient landmarks to guide them towards foraging or nest sites (e.g., Collett, Dillmann, Gieger, & Wehner, 1992; Wehner & Flatt, 1972), hatchling sea turtles find the sea by crawling towards the lowest, brightest feature in the environment (Lohmann & Lohmann, 1996), pigeons use olfactory cues (e.g., Able 1996; Wallraff 1981) and magnetic fields (e.g., Walcott & Green, 1974), and pre-industrial humans, such as the Polynesian navigators, use cloud patterns and reflected light as beacons when sailing between islands (Riesenberg, 1972).

Predatory attacks in which the predator has continuous information about the location of the prey can also be viewed as a form of beacon homing. Through sensory feedback loops predators can adjust their attack to account for evasive maneuvers of the prey. Wolves and lynx, for example, use visual feedback of their prey's movements to guide their attack. Many nocturnal owls utilize auditory feedback from the small rodents they hunt. Some sharks pinpoint the location of buried or otherwise hidden food items from the minute electrical impulses produced by the prey's muscular system. These examples indicate that beacon homing is quite important in predatory attacks. Predatory arthropods (including insects) make similar use of beacon homing to guide their attacks on prey items. Land's (1993) study of the pursuit tactics of the fly *Poecilobothrus nobilitatus* demonstrated the importance of visual feedback from the beacon (i.e., another fly) in guiding males as they chased females during courtship or other males that invaded their territories.

There are two ways to utilize sensory feedback from a beacon: continuously or discontinuously. In continuous feedback, input is constantly updated, while in a discontinuous feedback system input used to guide locomotion is periodically sampled and an executed movement is not altered by further feedback until the movement is completed. *Poecilobothrus nobilitatus*, for example, uses a continuously updated feedback system when chasing a moving target, whereas another fly, *Musca domestica*, utilizes a discontinuous system (Wagner, 1986). Nonflying predatory arthropods also make use of continuous or discontinuous feedback systems to guide their attacks.

Although the previous examples have dealt with visual feedback, other sensory modalities may provide beacon information in arthropods. Many arthropods make use of vibratory feedback to identify, locate, and guide their attack on their prey. Web spinning spiders, of course, are the classic example of vibrations serving as a beacon identifying prey location. During hunting, sand scorpions (*Paruroctonus mesaensis*) make use of two types of vibratory waves (compressional and Rayleigh waves), produced by their prey, burrowing cockroaches (Brownell, 1984). A complex series of vibratory receptors located in the scorpion's lower leg joints and exoskeleton allow the scorpion to home in on the prey's position and capture the buried cockroach.

Two groups of aquatic insects are also known to make use of vibratory stimuli produced by prey items during hunting. Murphey and Mendenhall (1973) and Murphey (1971a, 1971b) have shown that backswimmers (*Notonecta undulata*) and waterstriders, respectively, both utilize water surface waves to determine their prey's position. Like the sand scorpion, both of these insects have vibration receptors located in the tibial-tarsal joints of their legs. In a series of elegant studies Murphey (1971b) demonstrated that these vibration receptors are used to detect the position of the prey. When a waterstrider detects the surface vibrations produced by a small insect that has fallen onto the water and is struggling to escape the surface tension, the waterstrider orients so that it is pointed towards the prey.

Murphey's experiments with waterstriders were extremely controlled. Waterstriders were tethered in place by a fine coil spring affixed to the dorsal surface of their thorax. This allowed them to rotate in place, but prevented other movement towards the prey. Prey items (fruit flies and a mechanical vibration producing probe) were placed randomly on the water surface in an annulus 70-90 mm from the centre of the tethered waterstrider. Through a series of lesioning experiments, in which the tibial-tarsal joints were amputated, Murphey (1971b) investigated the limitations of the waterstriders' prey detection and orienting abilities. When all vibration receptors were intact waterstriders executed relatively accurate rotations towards the prey. With the lesioning of vibration receptors waterstriders made systematic rotational errors in response to the presence of the prey. Murphey showed that the errors could be understood by considering the angular positions of the waterstriders' legs. When the vibration receptor on the right metathoracic leg was lesioned the midpoint between the next closest receptors (i.e., on the right mesothoracic and left metathoracic legs) is about 135°[5] (see Fig 2-1). Consequently, with the right metathoracic leg lesioned, when the prey is located at a bearing of less than 135° the receptor on the right mesothoracic leg is the first to be stimulated. For prey situated at angles greater than 135°, the receptor on the left metathoracic leg is the first to detect the vibratory wave front. The result would be an underestimation of the angle of rotation or a rotation in the contralateral direction from the prey, respectively. Interestingly, Murphey found that lesioning right-side receptors, for example, had no influence on rotations towards prey items located on the left side of the waterstrider. It appears that the ability to use vibrations as guiding beacons during hunting could be controlled by some relatively basic underlying neural mechanisms in the waterstrider. Snyder's (1998) functionally equivalent artificial neural network model of

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[5] Note that angles are measured from the longitudinal axis of the waterstrider where 0° is directly ahead and positive angles are to the right and negative angles to the left.

Murphey's behavioural findings provides supporting evidence for the simplicity of the neuronal system controlling this beacon homing process.

There are, however, a number of interesting features that Murphey's studies did not address. First, as described, these experiments were quite controlled. Waterstriders could rotate but were unable to make translational movements. Consequently, only the rotational component of the first movement, or stride, made by the waterstrider towards the prey was recorded. The tethering process restricted the translational component of the first, and subsequent, strides made by a waterstrider attempting to reach the prey item.

The study detailed in this chapter sought to expand upon Murphey's original work. Experimental waterstriders were unconstrained and allowed to move freely throughout the testing arena. Although the trials were run in a laboratory, the freedom of movement of the waterstriders and the moderately sized arena makes this a semi-naturalistic study. Similarly, waterstriders were allowed to make multiple strides towards the prey item. This allows a comparison between the rotation of the first stride in Murphey's tethered and this unconstrained condition, as well as an analysis of rotational corrections for strides after the first. In addition, this protocol permits study of the non-rotational (i.e., translational) movement components of a waterstrider's attack on a prey item. Murphey's work demonstrated that waterstriders are capable of estimating the angular deviation between themselves and their prey, probably from vibratory information. A related, but unresolved, question is whether waterstriders are also capable of estimating the distance between themselves and a prey item during an attack. This study addresses this question.

It should be noted that waterstriders use vibratory information in a variety of behaviours besides hunting, including mating (Spence & Wilcox, 1986; Wilcox, 1972; Wilcox, 1979; Wilcox & Spence, 1986), and territoriality (Hayashi, 1985; Jablonski & Wilcox, 1996). As discussed in the first chapter, besides their vibration detection system, waterstriders also possess a well developed visual system (e.g., Bohn & Täuber, 1971; Dahmen, 1991; Dahmen & Junger, 1988). The visual system is known to be used for drift compensation, that is, maintaining a constant position relative to the shore on moving water (Fairbairn & Brassard, 1988; Junger, 1991; Junger & Dahmen, 1986; Junger & Varjú, 1990). It has also been suggested that vision may assist in prey detection and capture (Jamieson & Scudder, 1979). Hence, while it was expected that the vibratory cues from the prey served as the stimulus vector in this beacon homing task, the possibility that vision played some role in guiding waterstriders to their prey could not be ruled out.

To summarize, in this study I report the hunting behaviour, under semi-naturalistic conditions, of adult *Gerris remigis* waterstriders, in particular, the rotational and translational movements made in response to the presence of prey (i.e., under beacon homing conditions). The data supports the hypothesis that movements (i.e., rotation and translation) made by waterstriders during predation are non-random: significant positive correlations were found between the rotational and translational components of strides and the angular deviations and linear separations between waterstriders and their prey. I hypothesize that vibrations produced by struggling prey provide sufficient information for waterstriders to calculate both the angular deviation and linear distance between themselves and prey. Although the results of the study support the hypothesis, they do not rule out the use of other senses, especially vision, by waterstriders during predation.

Methods

The hunting behaviour of fourteen adult *Gerris remigis*, collected from Blackmud Creek in Edmonton, Alberta, Canada, was observed in a semi-natural laboratory setting. All observations were carried out in July 1997. The waterstriders were housed communally in groups of four or five in 30x45 cm^2 tanks filled to a depth of 8 cm with de-chlorinated water. An 18-hours-on, 6-hours-off overhead fluorescent light cycle was maintained in the colony room. When not being tested the waterstriders were provided with free access to food consisting of pre-killed (via freezing or decapitation) crickets (*Gryllinae sp.*), *Drosophila*, and tenebrionid beetles. Three days before testing, access to food was denied to ensure interest in the live prey items.

Prey items were worker *Formica* spp. ants. A 45 cm long fine silk thread, epoxied to the thorax of each prey item, was used to lower the live ant onto the water surface and remove it before it was captured by a waterstrider. Removal of the prey allowed several trials to be run sequentially with the same waterstrider without concern over satiation effects.

The testing arena was a circular plastic basin (40 cm diameter, 12 cm high wall) filled with 5 cm of de-chlorinated water. Waterstriders were tested individually and allowed ten minutes to acclimatize to the testing arena after being transferred from their home tank. A trial began with an ant being placed on the water surface at an arbitrary location. The ant was removed when the waterstrider closed to within about 2 cm. When sequential trials with the same waterstrider were conducted at least five minutes were allowed to pass between trials. After testing, waterstriders were returned to their home tanks and fed.

All trials were videotaped using a Sony Handycam model CCD-FX710 camera suspended 90 cm above the testing arena on a cantilever arm. Video footage was played back for analysis on a Sanyo VHR-9426A video cassette recorder (VCR). A piece of acrylic transparency was placed over the 19 inch monitor and positions of the waterstriders were traced onto the transparency for later analysis. The starting position of a waterstrider was recorded on the acrylic transparency just prior to its initial movement in the direction of the prey item. After Jamieson and Scudder (1979) the initiation of an attack was taken to begin with a rapid movement of a waterstrider towards the prey. Subsequent positions of a waterstrider were recorded on the transparency at the end of each movement phase, that is, when the waterstrider's forward movement stopped or when another powerstroke of the mesothoracic legs was initiated (see Figure 2-2). A powerstroke is defined as the thrust of one or both mesothoracic legs used to move a waterstrider on a stride. Each movement phase is referred to as a "stride" for purposes of this paper. A stride may involve rotational and/or translational movement of a waterstrider's body relative to the water surface.

Results

Although waterstriders combine both rotational and translational movements during a stride, the data concerned with rotational motion is presented first, followed by the data dealing with translational movement.

Rotational Movement

Figure 2-3A illustrates the relationship between the initial angular deviation of the prey from a waterstrider and the rotational movement of the waterstrider's first stride. It was observed that waterstriders generally make the shortest rotation necessary to minimize the deviation between themselves and prey. For example, if the prey was located 120° to the right of a waterstrider, the waterstrider would rotate 120° clockwise rather than 240° counterclockwise. Note, however, the five rotations depicted in the upper left and lower right quadrants in Figure 2-3A. When prey is nearly directly to the rear, waterstriders occasionally take the longer rotational path. Murphey's (1971b) experimental results and Snyder's (1998) simulation data show the same pattern. When these five points are excluded, a correlation of 0.98 ($R^2 = 0.97$) was obtained.

Similar rotations, used by waterstriders to match the angular discrepancy between themselves and their prey, are repeated in all strides after the first. Figure 2-3B depicts the waterstriders' rotations towards prey on their second strides ($R = .91$, $R^2 = 0.82$). Subsequent strides, although not shown, are similar. As is evident, the angular deviations at the beginning of the second stride (approximately ±75°) are less than those at the beginning of the first stride (approximately ±180°). Although not shown, this pattern of reduced angular ranges continues in subsequent strides, with the angular deviations covering ranges of ±60° and ±50° for the third and fourth strides, respectively.

Rotation accuracy can be gauged by the angular error of a turn. This measure is calculated by subtracting the angular deviation of the prey from a waterstrider's angle of rotation (Figure 2-4). Positive errors indicate over rotation and negative errors under rotation. Waterstriders under rotated slightly on the first two strides (stride 1: M = -6.1, SD = 27.06; stride 2: M = -6.0, SD = 13.49), but not on the third stride (M = 0.8, SD = 11.49).

Angular deviation and distance moved on a stride are plotted against rotational error in Figure 2-5A and 2-5B, respectively. In all cases the rotational errors (the absolute difference between the angular deviation and the angle rotated through by a waterstrider during a stride) show the greatest range for the first stride. For the first stride, as the angular deviation of the prey increases, so does the rotational error produced by a waterstrider (Fig. 2-5A). The second and third strides produce lower levels of rotational error, but also show reduced ranges of angular deviation. Following the first stride rotational error is relatively constant, with an upper range of about 20°. There were no strong correlations (R = 0.26, R = 0.071, and R = 0.021 for the first, second, and third strides, respectively) between the distance moved on a stride and the rotational error for that stride (Fig. 2-5B).

Translational Movements

The maximum distance tested for which a waterstrider responded to a prey item was 22 cm. A minimum of two and a maximum of seven strides were required for waterstriders to close to within about 2 cm of the prey items (Fig. 2-6), with most waterstriders taking three or four strides to reach prey initially located 7 to 15 cm away. There is a correlation of +0.63 ($R^2 = 0.39$) between the initial distance between the waterstrider and the prey and the number of strides waterstriders take to reach the prey.

A moderately high correlation of 0.69 ($R^2 = 0.48$) is found between the distance moved during the second stride and the distance remaining to reach the prey after the completion of the first stride (Figure 2-7). With one exception, maximum stride length was approximately 8 cm.

A similar matching of the stride length with the distance to the prey is seen in the third stride (Figure 2-8). When the linear movement of the third strides are plotted against the distance to the prey after the completion of the second stride, correlation is 0.83 (R^2 = 0.68).

Figure 2-9 plots the angular deviation of the prey and the rotation made by waterstriders against the distances moved during a stride. In most cases waterstriders move between 2 and 4 cm (M = 2.8 cm, SD = 1.8 cm) on their first stride, although there were a number of instances in which longer movements were made. In these cases, the prey items were located to the front of the waterstrider, at a maximum angular range of about ±100°. On the second stride the mean distance moved is 4.8 cm (SD = 1.7 cm), and for the third stride the mean distance moved is 3.0 cm (SD = 1.0 cm).

Discussion

Based on the results of this study I propose several strategies that *Gerris remigis* employ during hunting related to the detection and localization of live prey items. Different strategies may be employed when dealing with dead rather than live prey. It should be remembered that prey capture was not included in trials. Presumably additional strategies are employed when waterstriders attempt to grasp their prey with their prothoracic legs.

Waterstriders accurately match the angular deviation between themselves and their prey. Figure 2-3 displayed a high correlation between the angle of deviation of the prey before the stride and the angle rotated through during the stride. Such high correlations indicate that waterstriders have a highly accurate perceptual system that interprets information about the prey's location and calculates the appropriate angle for rotation for a stride. One result of this is that while waterstriders respond to prey at angles of ±180° on the first stride, the reduction of the angular deviation between themselves and their prey on the first stride reduces the angular deviation of the prey to ±70°, ±60°, and ±50° for the second to fourth strides, respectively.

It is also clear that waterstriders take the shortest rotational path to match their angle with the prey, thereby minimizing energy expenditure. A few exceptions occurred when the prey was more than ±160° off a waterstrider's midline axis (Figure 2-3A). While such rotations were somewhat erroneous, they still resulted in positioning a waterstrider with its head towards the prey after the completion of the rotation. In addition, because Murphey (1971a) demonstrated that waterstriders require more than one powerstroke from a mesothoracic leg to rotate through turns greater than 100°, whether a waterstrider rotates to the right 160° or to the left 200° still necessitates two strokes of the mesothoracic leg ipsilateral to the prey item.

Another strategy employed by waterstriders when matching their angle of rotation to that of the angle of deviation of the prey was to under rotate somewhat. On the first and second stride waterstriders show a slight tendency to under rotate (Fig. 2-4), that is, they do not often overshoot the angle of deviation of the prey. This may be advantageous in that it could allow waterstrider to use the angular momentum of their first rotation on their next stride. Continuing in the direction of rotation would be less energy expensive than overcoming momentum to rotate in the opposite direction, especially for large rotations that require powerful strokes of the mesothoracic legs.

Despite the general accuracy of angular matching demonstrated by waterstriders, there is still a certain amount of rotational error (i.e., difference between the target angular deviation of the prey and the angle rotated by the waterstrider) on any given stride. For the first stride the greater the angular deviation of the prey, the greater was the rotational error (Fig. 2-5A). On the second and third strides the mean rotational error droped to about 10° (as opposed to 21° for the first stride) with an upper level of about 20°, regardless of the angular deviation. The higher level of rotational error on the first stride was a direct consequence of the necessity for waterstriders to use multiple powerstrokes of their mesothoracic legs to rotate through angles greater than 100°. While waterstriders often execute the double powerstrokes in rapid succession, in some cases they pause before carrying out the second stroke of the mesothoracic leg. The strokes with pauses appear in

Figure 2-5A as high rotational errors at high angular deviations. When they are removed from the data set, the mean rotational error for the first stride falls to 14°.

Unexpectedly, no strong correlations were found between the rotational error and the distance moved on a stride (Figure 2-5B). I had anticipated that larger translational movements would produce elevated rotational error. Apparently the larger physical exertion required for large movements does not adversely affect rotational accuracy. Also, environmental factors, such as air and water currents, do not appear to increase rotational error on longer strides, at least not in the laboratory setting under which the trials were conducted. In a natural environment water currents and winds may have an impact on rotational accuracy.

With respect to the translational movements of waterstriders during hunting, the strategy employed appeared to be one of matching the stride length proportionally with the total distance to the prey, particularly when a waterstrider's head is roughly aligned with the prey (e.g., within ±70°). Positive correlations were found between both the initial distance to the prey and the number of strides taken to reach it (Figure 2-6) and the length of the second and third strides and the distance to the prey at the beginning of the stride (Figures 2-7 and 2-8). These results suggest that waterstriders were not moving randomly but were capable of representing the distance to a prey item and using this information to determine the length of their stride, up to some maximum.

Of the twenty-two presentations in which prey were more than 8 cm away from the waterstrider, in only one case did stride length exceed 8 cm. Thus, 8 cm may be a typical upper maximum to the length of a stride for *Gerris remigis* during hunting. Jamieson and Scudder (1979), who demonstrated a correlation between the leg length (the sum of the mesothoracic femur, tibia, and tarsus) and stride length, found that during non-hunting locomotion strides did not exceed 4 cm. The difference in maximum stride length during activities is not very surprising. During hunting one should expect more directed and energy expensive movements, especially for waterstriders which compete with one another for food resources (e.g., Blanckenhorn, 1991; Wilcox & Ruckdeschel, 1982).

It appears that maximum stride length can only be achieved within certain prescribed rotational ranges. When waterstriders rotate more about ±75° stride lengths are typically not more than about 4 cm (Fig. 2-9). This limitation only applies to the the first stride, for which waterstriders can experience angular deviations of prey above ±75°. On subsequent strides, waterstriders did not always achieve maximum stride length. Within the rotational limits described, the strategy appeared to be one of matching the stride length proportionally to the distance to the prey, up to a maximum.

Waterstriders also appear to take the distance remaining to the prey into account in an effort to avoid overshooting the prey's position. In all but three cases shown in Figure 2-8, a maximum stride length of 8 cm would have carried the waterstrider past the prey. If a waterstrider overshoots its prey, the probability of capturing the prey is dramatically reduced because it must take the time to turn around (Jamieson & Scudder, 1979). Therefore, it advantageous for a waterstrider to move so that it keeps the prey to the front, at least until the waterstrider is close enough to grasp the prey with its prothoracic legs.

To summarize, waterstrider hunting strategy appears to consist of two primary features: matching the angle between the waterstrider and the prey and proportionally matching the stride length to the distance to the prey. When matching the angle, waterstriders rotated towards the same side as the prey was on through the shortest rotational arc. Also, on the first stride it is unusual for a waterstrider to over rotate past the prey, although this does not appear to hold for later strides. Following the first stride, the lengths of subsequent strides are fairly strongly correlated with the distance to the prey, up to a maximum length of about 8 cm. Although longer strides do not add increased rotational error, waterstriders do not necessarily move the maximum length.

To this point I have focused on the strategies used by hunting waterstriders but have not concerned myself with the type of information waterstriders utilize to make determinations about angles and distances to the prey. The two principle sources of information that waterstriders could use to detect and locate prey are vibratory and visual. In this experiment, prey items potentially provided both vibratory and visual stimuli. Thus, vibratory cues may not have been the only source of information waterstriders used to detect and locate live prey while hunting. That vibratory stimuli give *sufficient* information for waterstriders to effectively hunt was already discussed.

Waterstriders (Murphey, 1971b), as well as other aquatic insects (e.g., Murphey & Mendenhall, 1973; Wiese, 1972) and terrestrial arthropods (Brownell, 1984), have vibration detecting (i.e., wave detecting) receptors in the joints of their legs. Murphey (1971b) suggested that these receptors are non-directional in nature; they can detect a vibration but can not, individually, determine directional information about a vibration. Instead, the receptors act in combination. Using this constraint, Snyder's (1998) simple artificial neural network (ANN) model of waterstrider rotation towards prey supports the premise that vibratory information from multiple receptors is centrally integrated in making an accurate angular estimation. The ANN, using only temporal differences in the detection of a vibration wave front across receptors, produced patterns of rotation functionally equivalent to the behavioural findings in Murphey's lesioning studies. Thus, the ANN modeled the behavioural data successfully using vibratory input alone.

Furthermore, in Murphey's (1971b) study prey were dropped on the water surface 7-9 cm away from the waterstriders. When no vibration receptors were lesioned, waterstriders made rotations towards the prey similar to those depicted in Figure 2-3. When vibration receptors were lesioned, however, waterstriders made systematic errors, indicating that the receptors are crucial for determining the angular deviation of the prey. If the visual system were also involved in identifying the prey's location one would expect the errors in rotation caused by lesioning vibration receptors would not have occurred, or at least would not have been so pronounced. Murphey's results do not indicate that the visual system was not used by waterstriders during hunting, although they do imply that if vision were used, it would be at distances of less than 7 cm. This is one piece of evidence that supports the suggestion that vibrations produced by the prey could also provide sufficient information for waterstriders to accurately calculate the distance to the prey. Waterstriders may use visual cues from the prey during the final stages of predation when they are engaged in actually capturing the prey with their prothoracic legs. The next chapter addresses the question of the importance of visual and vibratory stimuli for guiding waterstriders towards their prey under beacon homing conditions.

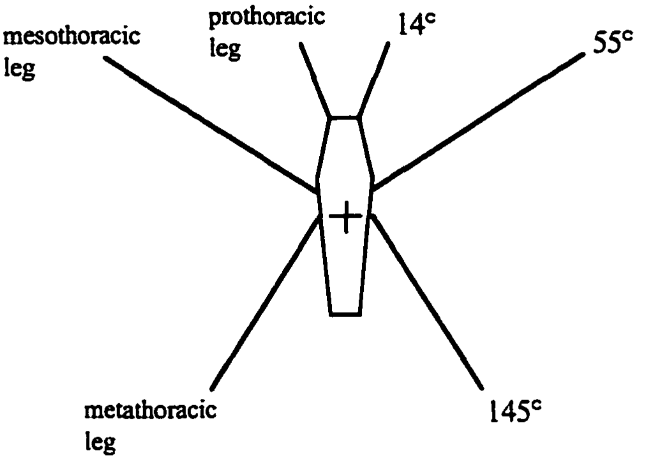

Figure 2-1: Schematic diagram of waterstrider listing leg names and approximate angular location of tibial-tarsal vibratory receptors for legs.

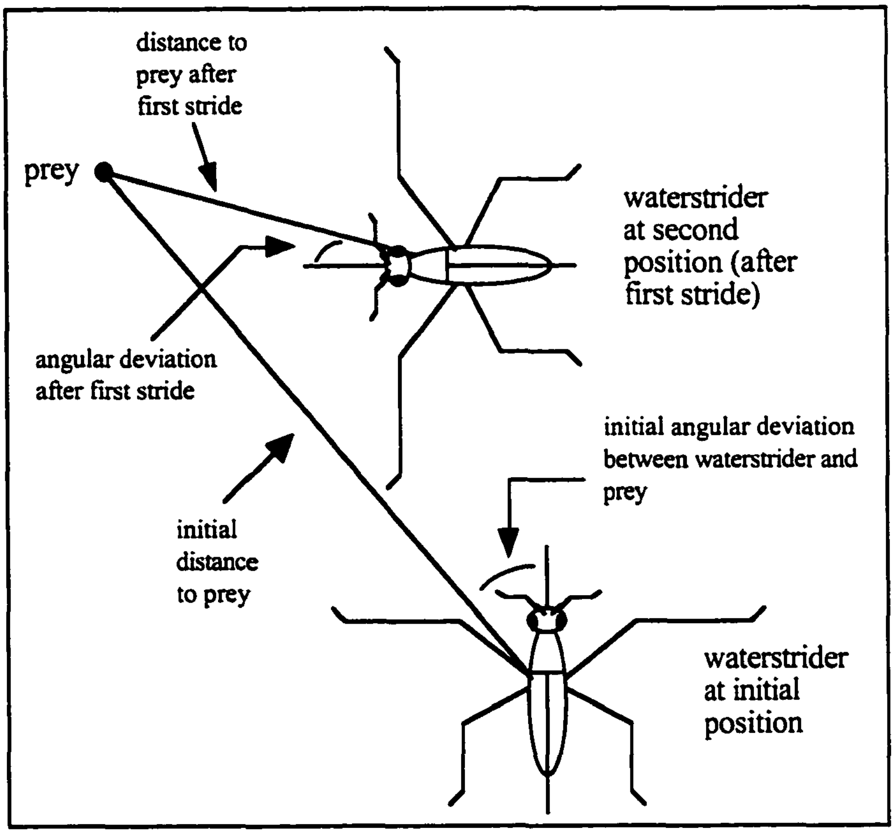

Figure 2-2: Schematic representation of angular and distance measurements. Distances are measured from the centre of the prey to the centre of the waterstrider. Angular deviations are between 0° to ±180°, with positive/negative angles to the right/left of the longitudinal midline of the waterstrider, respectively. Waterstrider rotations use the same notation (i.e., 0° to ±180°), with clockwise rotations being positive and counterclockwise rotations negative. A stride is defined as beginning with the movement of a waterstrider out of its "resting position" and concluding with the return of a waterstrider to its resting position.

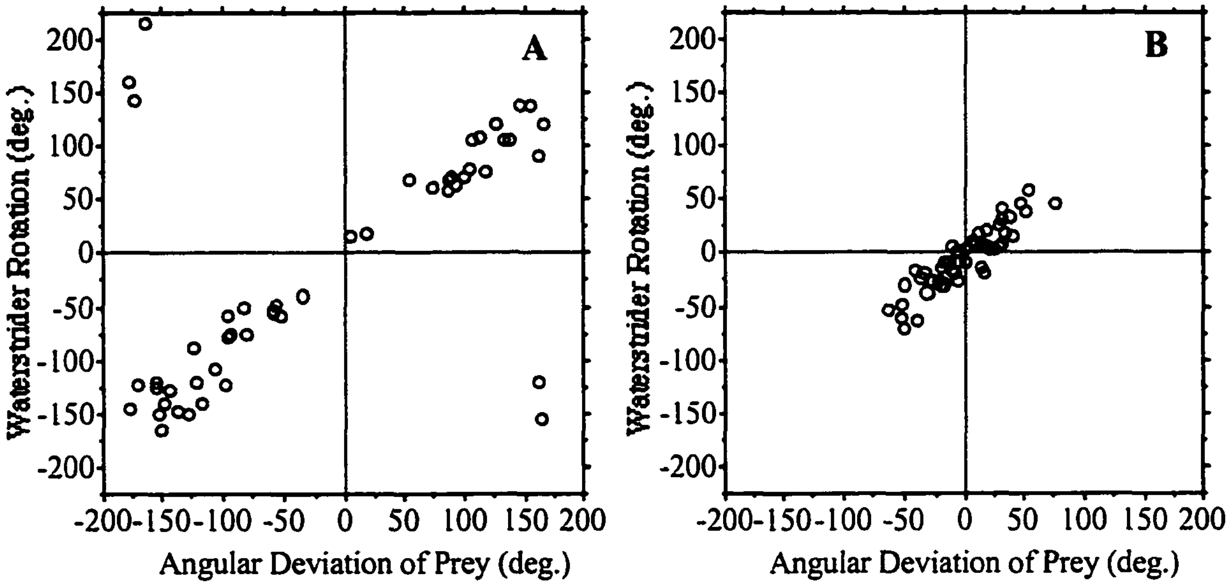

Figure 2-3: Rotational component of waterstrider strides. A. Angular deviation of prey versus the angle of rotation made by the waterstriders for the first stride. B. Angular deviation of prey versus the angle of rotation made by the waterstriders for the second stride.

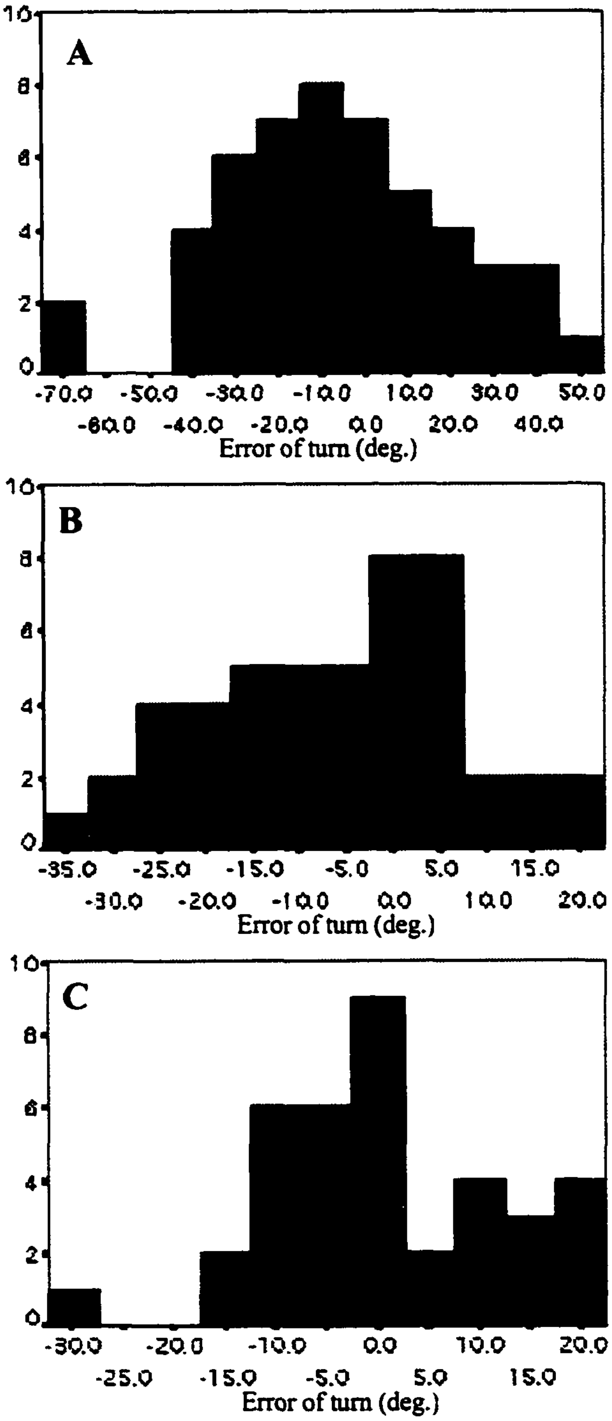

Figure 2-4: Accuracy of rotations. Error of turn is a waterstrider's rotation minus the angular deviation of the prey. A: first stride. B: second stride. C: third stride.

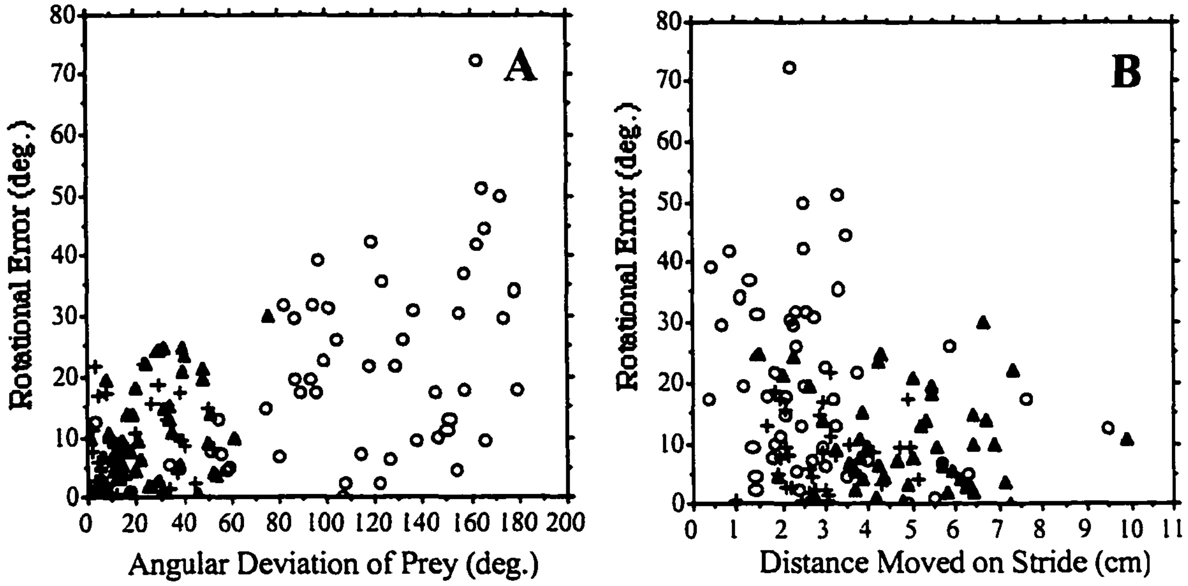

Figure 2-5: A: Absolute angular deviation of prey before a stride versus the absolute rotational error during that stride. B: Distance moved on a stride versus the rotational error produced during that stride. Rotational error is the absolute value of the difference between the angular deviation of the prey and the angle rotated by a waterstrider during a stride. Open circles represent the first, closed triangles the second, and crosses the third strides.

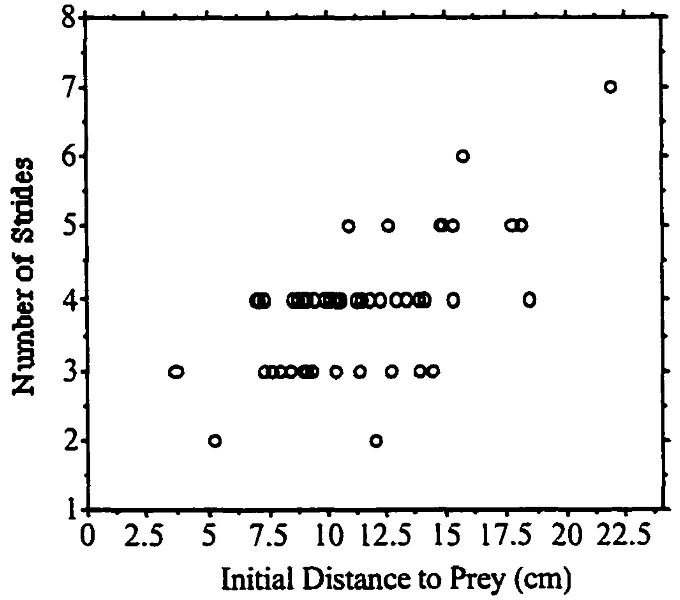

Figure 2-6: Initial distance to prey versus the number of strides required to bring waterstriders within < 2 cm of the prey.

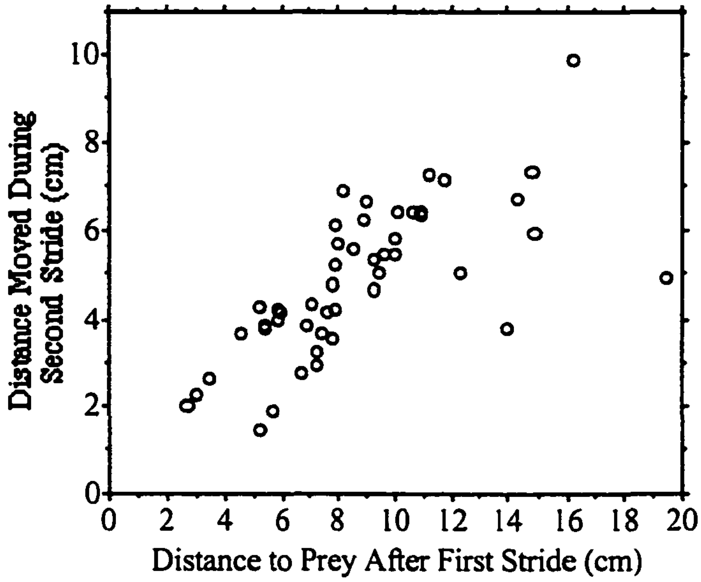

Figure 2-7: Distance between prey and waterstrider after the completion of the first stride plotted against the distance moved by the waterstrider during the second stride.

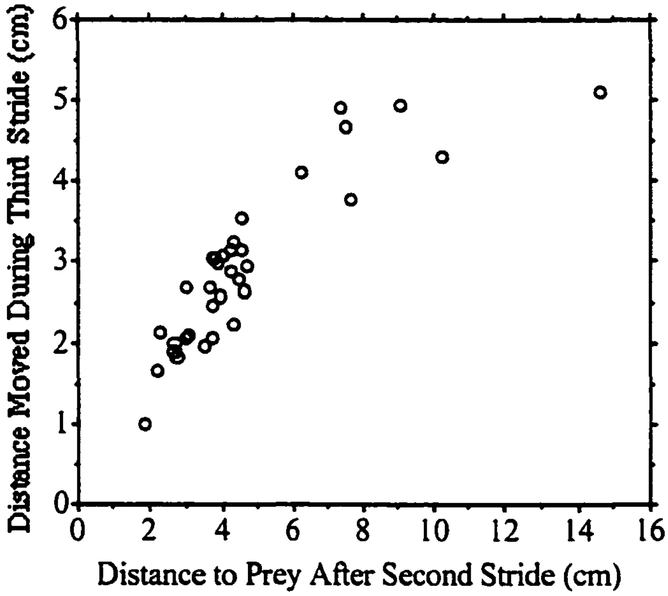

Figure 2-8: Distance between prey and waterstrider after the completion of the second stride plotted against the distance moved by the waterstrider during the third stride.

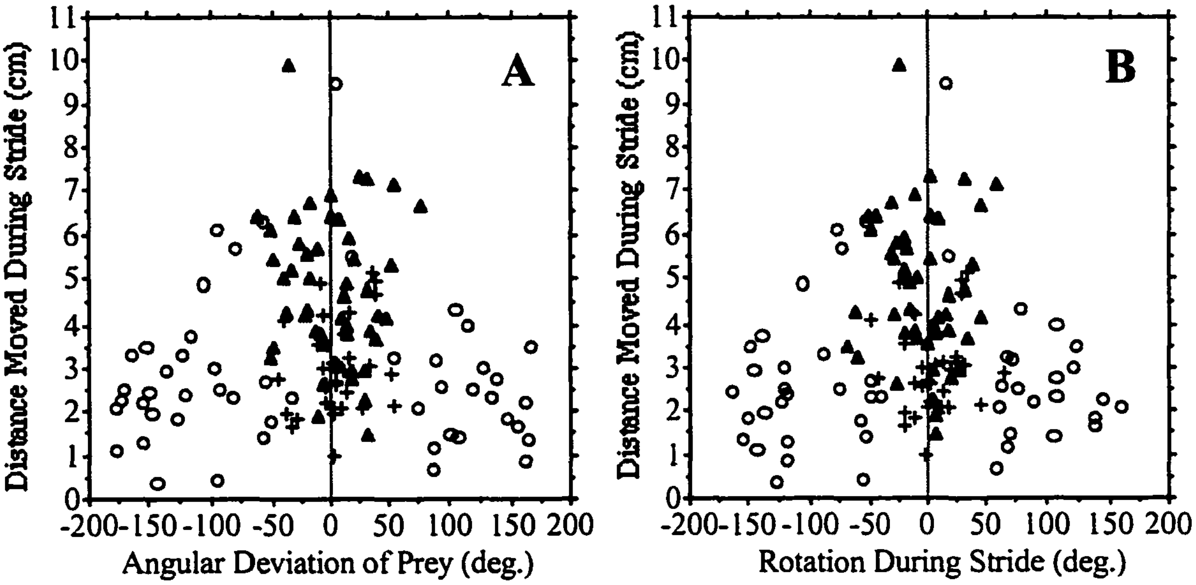

Figure 2-9: Angular-deviation of prey versus against the distance moved during a stride. B: Rotation of waterstrider during stride versus the distance moved during a stride. Open circles represent the first, closed triangles the second, and crosses the third stride.

Chapter 3:

The Importance of Visual and Vibratory Cues for Determining the Position of Prey

Introduction

The previous chapter reported on the attack behaviours of hunting waterstriders under beacon homing conditions. In the study no controls were placed on the sensory input from the prey available to waterstriders. The two obvious sensory modalities waterstriders can use to localize the position of prey are vibratory and visual. Although Murphey (1971b) argued from his lesioning studies of waterstrider vibration receptors that surface waves provide the primary information guiding an attack, Dahmen (1991) and Jamieson and Scudder (1979) suggested that visual cues can also be used in detecting and localizing prey during hunting. The purpose of this study is to determine if visual feedback from the prey is needed by *Gerris remigis* during hunting.

Separating visual and vibratory input from a prey item to a hunting waterstrider is challenging. The most obvious solution is to simply cover the compound eyes of waterstriders with black paint. This, however, raises the risk of confounding behavioural processes. For example, at night waterstriders either leave the water surface or anchor themselves with a foot to some stationary object in the water, such as a reed or rock. Because their drift compensation mechanism is visually mediated, waterstriders can not identify the landmarks needed for place fixing in the dark, and will drift downstream, as demonstrated by Junger and Varjú (1990). However, Wilcox (1979) showed that waterstriders temporarily blinded with tiny rubber eye patches were able to identify males from females for the purpose of mating. Nevertheless, for this study methods other than blinding were used to remove visual information about the prey from the waterstriders.

This chapter contains information derived from two studies. The first experiment was behavioural in nature. Waterstriders were tested with live prey under various sensory conditions. Visual and/or vibratory stimuli produced by prey were either blocked from, or made available to, waterstriders to test their ability to initiate attacks on prey and the accuracy of attacks. The second study involved the use of a computer simulation to examine whether the curvature or amplitude of surface waves produced by struggling prey would provide better information for waterstriders attempting to determine the prey's position.

Experiment One: Behavioural Study

Methods

The hunting behaviour of ten adult waterstriders (*Gerris remigis*) was observed under laboratory conditions. The waterstriders, collected from streams in the vicinity of Edmonton, Alberta, Canada, were housed communally in groups of five in 30x45 cm^2 tanks filled to a depth of 8 cm with de-chlorinated water. Each tank was equipped with an airstone to help keep the water surface clean. The tanks, covered with a fine wire mesh, were placed outdoors, providing the waterstriders with natural lighting and weather conditions. When not being tested the waterstriders were fed on pre-killed crickets. Three days prior to testing, access to food was denied to ensure interest in prey items.

Prey items were worker *Formica* spp. ants. A 50 cm long fine silk thread, epoxied to the dorsal thorax of each prey item, was used to lower a live ant onto the water surface. This allowed accurate placement of the prey item and prevented the ant from breaking the surface tension of the water and sinking, as could happen if the prey item were simply dropped onto the water surface.

Barrier type and placement blocked or permitted waterstriders access to different sensory information about the prey's position (Talbe 1). The testing arena was a 40x40 cm^2 Plexiglas tank with 15 cm high walls. The testing arena could be divided in half by either a transparent or opaque (i.e., black) Plexiglas guillotine barrier that spanned the width of the arena. The opaque barrier blocked the transmission of the visible spectrum. Barriers were situated so that their lower edge was positioned either 2 cm below or 1 mm above the water surface. This produced the four experimental conditions with the barrier: transparent-above, transparent-below, opaque-above, and opaque-below. A control condition was also carried out in which no barrier was present.

Waterstriders were tested individually. After the appropriate barrier was put in place, a waterstrider was placed on one side of the arena and allowed ten minutes to acclimatize to its surroundings. A trial was only started if the waterstrider was still and not grooming. On each trial an ant was lowered onto the water surface on the opposite side of the barrier as the waterstrider. After the waterstrider responded to the prey by initiating a hunting response, or if the waterstrider failed to respond after 10 seconds, the prey was removed, ending the trial. One minute was allowed to elapse before the next trial was begun. To prevent extinction of a waterstrider's hunting response no more than five presentations of a prey item were made in a single testing block. After testing, waterstriders were returned to their home tanks and fed. Because of the barrier, waterstriders were unable to actually reach the prey. In the control condition (no barrier present) prey were lifted from the water surface when a waterstrider closed to within 2 cm.

All trials were videotaped using a Sony Handycam camera (model CCD-FX710) suspended 100 cm above the testing arena on a cantilever arm. Video footage was played back for analysis on a Sanyo VHR-9426A video cassette recorder. A piece of acrylic transparency was placed over the 19 inch television monitor and positions of waterstriders and prey were traced onto the transparency for later analysis. The starting position of a waterstrider was recorded on the acrylic transparency just prior to its initial movement in the direction of the prey item. After Jamieson and Scudder (1979), the initiation of hunting response was taken to begin with a rapid, directed movement of a waterstrider towards the prey. Starting positions for each subsequent "stride" (the movement produced by a powerstroke from a waterstrider's mesothoracic legs) were recorded on the transparency. A stride may contain rotational and/or translational movement of a waterstrider's body relative to the water surface. Recording was stopped after a waterstrider came in contact with the guillotine barrier.

Results

When waterstriders responded to the presence of a prey item the initiation of their hunting response typically began no more than two seconds after the prey was lowered onto the water surface. Because of the presence of the barriers, it was impossible for a waterstrider to actually reach the prey item. Nevertheless, on most trials waterstriders completed two strides before the barrier stopped their movement.

An attack was determined to have occurred if the waterstrider took a stride that moved it closer to the prey's position within ten seconds of the prey being placed on the water surface. In the event that the waterstrider did not move towards the prey or did not move at all, within the ten second time limit, the trial was recorded to have produced no attack.

Barrier below surface

In both conditions in which the transparent and the opaque barriers were positioned below the water surface, no waterstrider initiated an attack on a prey item. Sixty-three trials were conduced with the transparent barrier and 55 with the opaque barrier. In all instances, waterstriders showed no indication that they detected the presence of a prey item on the other side of the barrier.

Barrier above surface

Waterstriders responded to the presence of prey items when both the transparent and the opaque barrier were positioned above the water surface, initiating typical hunting responses. In all trials waterstriders initiated attacks towards the prey within the ten second time limit. The hunting response of waterstriders can be characterized as a series of rotational and translational movements, that is, a series of strides, that minimize the distance between a waterstrider and its prey. As such, one may discuss angular changes in the position of a waterstrider's body axis before and after a stride relative to some external point of reference, in this case, the position of the prey item.

Figure 3-1 shows the relationship between the angular deviation of the prey items prior to, and the rotational movement of the waterstriders during, the first stride for the two experimental conditions in which the barrier was located above the water surface and for the control condition. In all cases, waterstriders rotated so as to attempt to match the angular discrepancy between themselves and their prey. Responses were the same regardless of the absence of a barrier or the presence of the transparent or opaque barrier. Rotation to bring the head more in-line with the position of the prey was continued by waterstriders in subsequent strides. Figure 3-2 shows the waterstriders' rotations towards the prey made on the second stride.

Figure 3-3 shows the linear movements of the waterstriders' second stride compared to the total distance to the prey. Because the first stride usually involved large rotational movements, the linear distances covered do not show a strong correlation with the total distance to the prey. Consequently, a better comparison was the linear distance moved during the second stride to the distance to the prey after the completion of the first stride. As in the study described in chapter two, these results indicated that waterstriders adjust their stride length based on the distance to the prey.

Discussion

In the absence of visual cues, vibrations produced by live prey items on still water provide sufficient information for waterstriders to identify the presence of prey and determine the prey's position. When barriers (transparent and opaque) were placed below the water surface, thereby blocking the transmission of vibrations, waterstriders initiated no hunting responses at all. This suggests that, at least under the conditions present in this study, surface vibrations are necessary for *Gerris remigis* to initiate hunting. When the barriers were positioned above the water surface no differences in hunting responses were seen whether the barrier was transparent (allowing both vibratory and visual information about the prey to reach the waterstrider) or opaque (preventing the waterstrider from detecting the prey visually). Thus, visual input is not necessary for a waterstrider to identify the presence of prey and to successfully determine the position of the prey relative to itself.

The fact that visual cues from the prey were not necessary for waterstriders to locate prey items does not mean that waterstriders do not rely on vision. Quite the contrary; waterstriders have a well developed visual system (e.g., Bohn and Täuber, 1971; Dahmen, 1991; Dahmen & Junger, 1988). Guthrie's (1961) anatomical study of the *Gerris* nervous system demonstrates that over 85% of their central nervous system is comprised of optic lobe. In particular, waterstriders' visual system is well known for its importance in drift compensation, allowing waterstriders to maintain a constant position on a moving body of water relative to the shore (Fairbairn and Brassard, 1988; Junger, 1991; Junger & Varjú, 1990).

What, then, of suggestions (e.g., Jamieson & Scudder, 1979) that waterstriders use their visual system to some degree during predation? Waterstriders would appear to have the visual acuity necessary to detect relatively small objects at short distances (e.g., Junger, 1991; Junger & Varjú, 1990). In addition, waterstriders feed opportunistically on carrion found on the water surface. Since already dead prey do not produce vibrations it stands to reason that waterstriders locate these food items visually, although olfaction could play a role. Personal observations suggest that detection of carrion is different from that of live prey, with live prey being detected more reliably and at a much greater distance than carrion.

Species of waterstriders may differ in their use of the visual system in hunting. Several non-predation related experiments by Spence and Wilcox (1986) support this possibility. They examined the mating system of two species of waterstriders and found that *Limnoporus dissortis* males were unable to determine the sex of other waterstriders visually and depend entirely upon the detection of repel ripple signal vibrations generated by other males for determining the sex of a waterstrider. When an *Limnoporus dissortis* male approaches another waterstrider, if no repel signal is produced the male proceeds with mating behaviour. *Limnoporus notabilis* males, however, appear to be at least partially capable of using visual cues to determine the sex of another waterstrider. *Limnoporus dissortis* and *Limnoporus notabilis* are closely related hybridizing species. The fact that they show differences in the use (or acuity) of their visual system suggests that the use of vision during foraging could be species specific. Hence, Jamieson and Scudder (1979) may have observed evidence of visually guided hunting in some of the *Gerris* species they were working with, but not with *Gerris remigis*, the species used in this study.

If the proposal that vibratory signals provide sufficient information for waterstriders to determine the angle and distance between themselves and their prey is correct, the question becomes one of how vibratory information is used. I suggest two methods that could be employed by waterstriders, each presumably within the capabilities of their nervous system.

One method waterstriders may use to determine the position of a prey item involves the curvature of the wave front generated by the prey. The closer one is to a point source that produces a water wave, the greater the curvature of the wave front. An estimation of the curvature of a wave front can be used to calculate the radius of the wave from the source that produced it. Waterstriders could exploit this property of waves for distance determinations

The curvature of a wave front could be determined by the variation in the time at which a wave front stimulates the vibration receptors of at least three of a waterstrider's legs. The system might operate as follows: stimulation of the first receptor is marked on biological endogenous clock. Stimulation of subsequent receptors are timed in relation to this event. Using this information, a waterstrider's nervous system could calculate the curvature of the wave front and produce an estimate of the angular deviation between and the distance to the source of the vibrations.

A waterstrider must determine the position of the prey relative to itself before it can determine either the angular deviation of the prey or the distance to the prey. One way this could be done is based upon the fact that the perpendicular bisector of a chord of a circle passes through the centre of the circle. It takes two points on the circle to determine the chord, and hence the perpendicular bisector. But the bisector does not determine the centre of the circle on its own. With a second bisector, requiring a third point on the circle, the intersection of the bisectors is the centre of the circle (see Figure 3-4). Hence, three legs (i.e., three vibration receptors) are required to make such a calculation. If, as discussed, a waterstrider can determine the time between the wave crests passing under its legs, when one leg is on a crest it can determine the position in space of the crest for the other two legs. Once this is known, the distance and angular deviation between the waterstrider and the prey can be calculated.

Another possibility is that waterstriders make use of the amplitude of the wave front to calculate the angle and distance to the source of the vibration. Murphey (1971b) briefly suggested that wave amplitude could provide essential information for hunting waterstriders. While wave front curvature flattens with distance, wave front amplitude decreases asymptotically. Thus, the further the source of a vibration, the smaller the wave's amplitude and hence the less vibration stretch receptors located in the joints of a waterstrider's legs would be stimulated.

Adult *Gerris remigis* have a tip-to-tip leg span of up to about 2.5 cm. As such, the wave front could decrease in amplitude sufficiently for the first leg contacted by the wave front to indicate a larger amplitude than the last leg contacted by the wave front. Murphey (1971b) estimated that surface vibrations in the appropriate frequency range would damp to half their amplitude within 2-4 cm. Based on the asymptotic decrease of the amplitude across the span of their legs, waterstriders could use this information to calculate the distance to the source of the vibration.

At present, it is not known what mechanism a waterstrider uses to determine the distance between itself and its prey. Either of the two methods hypothesized, or some combination of them, are feasible. As such, this as an interesting question for a simulation study using a connectionist artificial neural network (ANN). This type of modeling can provide valuable insight into the way relatively small nervous systems are capable of organizing themselves so as to produce adaptive behaviours in complex environments. The ANN model used here allowed an examination of which of the hypothesized angular and distance mechanisms is most accurate and what input information is actually required for angle and distance estimation.

ANNs can be defined generally as nformation processing systems whose architecture is patterned on biological nervous systems. ANNs, like biological nervous systems, comprise a number of simple processing units that transmit information through a series of interconnecting links with variable weights or strengths. Processing units in an ANN are typically viewed as being analogous to neurons.

To extend this analogy, the weighted connections between processing units in an ANN are usually described as fulfilling the same function as synapses. The connection itself is merely a communication channel; it is the weight associated with a channel that determines the nature and strength of a connection. For example, inhibitory connections are defined with negative weights and excitatory connections are defined with positive weights. The strength of the connection is defined by the size (i.e., absolute value) of the weight. The pattern of connectivity in an ANN (i.e., the network's entire set of connection weights) defines the causal relations between the network's processors and is therefore analogous to a program in a conventional computer (e.g., Smolensky, 1988). Unlike traditional computer architectures, however, ANNs are trained, or taught, rather than programmed.

ANNs are designed in multiple layers (see Rumelhart & McClelland and the PDP Research Group, 1986). The first layer, consisting of input units, is often considered to carry out a function similar to that of the sensory nervous system. Successive layers serve as additional processing elements, with the last layer being made up of output units which provide the answer to the pattern classification problem presented to the ANN. Caudill and Butler (1990) have noted that the most complicated neurocomputers are capable of mimicking the action of only a million or so neurons. They also note that this is about the same number of neurons present in the brain of a fly. For this reason they suggest, only half in jest, that artificial neural networks possess "fly power" (p. 5).

ANNs, or connectionist networks, are useful modeling tools for a number of behavioral problems and neurophysiological studies in general. While it is possible to construct detailed models of the interactions of individual neurons, these models become so constrained by the need to supply all parameters required to predict the response of individual neurons that such models are only applicable to the simplest of nervous systems. ANNs, however, provide a good compromise. They do not attempt to emulate all of the details of the neurons involved in the neural circuits of interest. Rather, an ANN focuses on the importance of connections between neurons, allowing more complex behavioral systems to be modeled from a neuronal perspective.

Experiment Two: Computer Simulation

Methods

The neural networks were created using 4.05 Neural Works Professional II Plus™. The networks were trained using a backpropagation rule with a full complement of legs to rotate towards the source of a vibration. Backpropagation, or the generalized delta-rule, is a common method for training ANNs (Rumelhart, Hinton & Williams, 1986). When the input units of the network are activated with a pattern, signals go up through the interconnections to the output units. The network then compares the output it calculated to the desired output. The difference becomes an error signal that is used to modify the weights. The error signal is then sent back down through the layers. The next time the signal is presented to the network the error will be reduced. Eventually, the network becomes structured and learns to give correct responses to the stimuli presented to it.

Two network architectures (see Figure 3-5) were tested. All networks consisted of a layer of input units and a layer of output units. No hidden units were used.[6] Each input unit was connected to each output unit. The type 1 networks had six input units and two output units, where each input unit corresponded to a vibration receptor in one of a waterstrider's legs and the output units gave the angle and distance of the target in X and Y coordinates. Leg orientation and vibration receptor positions were based on an idealized model of a waterstrider (see Figure 2-1). The type 2 networks had six input units and three output units. Input units served the same function as in the type 1 network, but the output units were expanded so that the first two gave the angle of the target in X and Y coordinates while the third output unit reported the linear distance to the target. Curvature and amplitude trials were run on both type 1 and 2 networks.

All receptors were assumed to be continuously in contact with the water surface, and individual receptors were taken to be nondirectional in their sensory capabilities (i.e., receptors only indicate whether or not they are stimulated, not the direction from which the stimulation occurs). For curvature trials distances from the source of vibrations to each leg tip comprised the input to the network. As in Snyder (1998), I hypothesized that waterstriders make use of timing differences between the stimulation of the leg receptors encountering a surface wave front, where the timing count begins with the first receptor to be stimulated. However, for purposes of calculation, I exploited the fact that the speed at which a wave front propagates and the distance it travels are linearly related. Therefore, the input to the network was the distance (in millimeters) of the prey to the receptors, standardized so that the closest receptor's distance was set to zero (i.e., the beginning of the timing count) and all other input distances had the closest receptor's distance subtracted from them.

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[6] In ANN terminology, input units receive information and output units return the computed result. Hidden units are processors that receive information from the input units, process it, and pass the result to the output units. A network must have input and output units; hidden units may or may not be required. Generally, the more complicated the processing task the more hidden units will be required

For amplitude trials, the amplitude of the wave front at each leg tip comprised the input to the network. Small surface waves of the order produced by a insect struggling on the water surface operate in a somewhat different manner than larger waves, typically dealt with and described by standard physics calculations. For small waves, called capillary waves, with amplitudes on the order of millimeters, gravity can be neglected and only surface tension becomes a factor in wave form calculations (Thewlis, 1961, vol. 1, p. 565). However, for the immediate purposes of this study an accurate representation of the amplitudes experienced by a hunting waterstrider are not necessary as the immediate question is whether or not an ANN can make appropriate rotational and distance estimations using amplitude and/or curvature information. Therefore, in this study the calculation of amplitude was somewhat simplified and was set to drop off as one over the square root of the distance.

Five networks of each type were separately trained and tested on each of the test conditions. Networks were trained on data sets of 400 randomly positioned targets between 30 and 100 mm from the centre of a waterstrider. Networks were trained for 10,000 iterations of the set, or until the network converged on a solution. That is, the set of 400 targets were presented to the network 10,000 times, the target order randomized for each presentation. Testing sets consisted of 200 randomly positioned targets, in the same 30 to 100 mm range as the training sets, presented to a network only once.

Results

Angles

Type 1 and 2 networks were able to accurately calculate the target angle using either curvature or amplitude information equally well (Figures 3-6 and 3-7).

Distance

Type 1 networks failed to calculate the distance to the target correctly (Figure 3-8). When curvature information was used type 1 networks produced distances that varied tightly around the median training distance, regardless of the actual distance to the target. Amplitude information also failed to result in correct estimates of distance. In this case the networks provided distances negatively correlated with the actual distance to the target.

Type 2 networks using curvature produced the same results as their type 1 counterparts; that is, they failed to give an appropriate estimate of the distance to the target (Figure 3-9A). However, when amplitude information was used with type 2 networks, a functionally equivalent estimate of target distances was achieved (Figure 3-9B). Functionally equivalent systems mimic behaviour although they do not necessarily represent the nervous system accurately (Fodor, 1968; Steels, 1993).

Discussion

Snyder's (1998) ANN simulations of waterstrider orientation to prey proposed that wave front curvature provided sufficient information from which waterstriders could estimate the angular deviation between themselves and their target. The present network study, however, suggests that wave front amplitude could be more useful for waterstriders, at least in terms of distance estimations. What is particularly interesting from this series of simulation studies, is that the networks fail to make correct distance calculations using curvature data, although mathematically either curvature or amplitude can be used to determine the correct distance to a target. Possibly, this is a factor of the physical size of a waterstrider. Because of the relatively small separation of the legs, waves originating more than a few centimeters away from a waterstrider may all appear to be flat, thereby eliminating the ability of curvature to provide useful information in distance calculations. This is not an entirely satisfying option, however, as the networks have no difficulties providing accurate angular estimations from curvature input. In addition, the hypothesis that curvature information is used in calculating angles should not be abandoned yet, as the simulations in the current study did not explore the effects of lesioning receptors as in Snyder (1998). Additional studies exploring the effects of lesioning, as well as the possibility that curvature and amplitude input are used in conjunction, should be conducted.

Another interesting feature of these simulation trials is that neither curvature or amplitude information could be used to make accurate distance estimations with a type 1 network. Only type 2 networks, that had three output units, using amplitude input provided proper values for the distance to the targets. In type 2 networks the first two output units provided the X and Y coordinates of the target, respectively, and the third output unit gave the distance to the target. The implication of this finding is that angular and distance calculations are made separately. Cheng's (1998) recent work with honeybees indicates that these insects store angle and distance information about a target (e.g., a food source, the hive, etc.) as separate elements in spatial memory. The present network simulations may reflect an underlying information processing feature of small neuronal systems dealing with directional data that shapes spatial memory organization.

It is important to recognize that the ANNs used to model distance estimation here were remarkably simple systems. For instance, no hidden units were required to solve the distance estimation problem in the type 2 network using amplitude information. In this case, the inclusion of additional hidden units, which can increase a network's processing power, would not markedly improve performance by the type 2 network tested with amplitude input. Generally, if a simpler system, for instance, one without hidden units, can solve a problem then increasing the complexity of the network architecture is of limited value. Snyder (1998), for example, found that the addition of hidden units did not improve the ANN's ability to determine angular deviations of prey items.

There is the possibility that the inclusion of hidden units may have improved ANN performance for type 1 networks or for type 2 networks using curvature input. However, the immediate interest of this study was to examine whether or not a such a simple ANN architecture could, in fact, provide accurate distance estimations with curvature or amplitude information. In this case, there is no specific information available about the neural circuitry involved in the vibration reception and interpretation systems of waterstriders. Similar approaches have been successfully applied to other insect systems for which limited neurological detail is available. Krakauer (1995), for example, has used a simple network model to investigate spatial memory in bees. One of the values of beginning with very simple network architectures is that they can provide an idea of the minimal levels of complexity required to accomplish a task.

Condition	Available Stimuli
control	vibrations, visual
transparent-above	vibrations, visual
transparent-below	visual
opaque-above	vibrations
opaque-below	none

Table 3-1: Experimental conditions and stimuli available to waterstrider for prey localization in each.

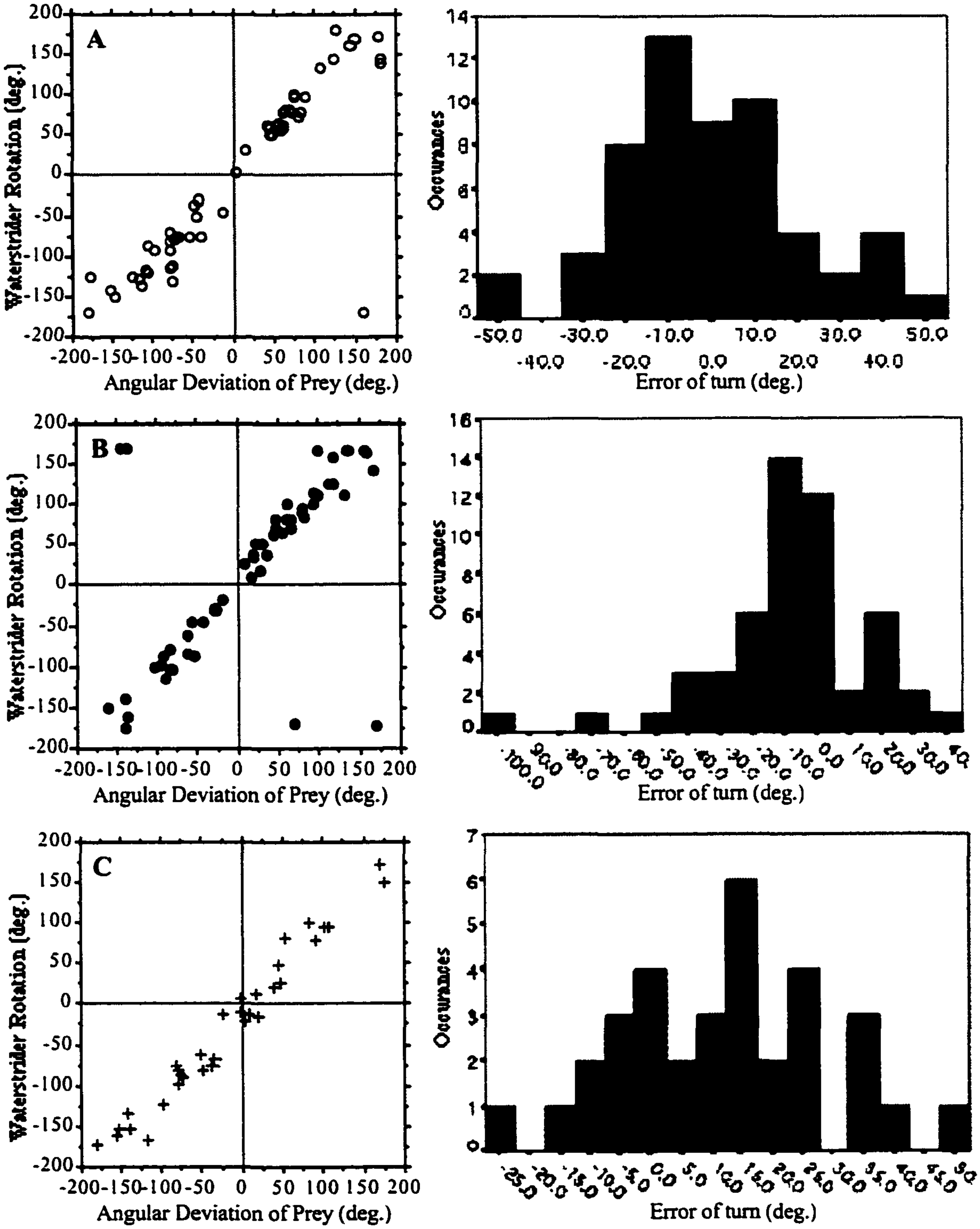


Figure 3-1: Left: Rotational component of waterstriders' first strides, showing angular deviation of prey versus the angle of rotation made by the waterstriders. Right: Accuracy of rotations. Error of turn is a waterstrider's rotation minus the angular deviation of the prey. Positive error indicates over rotation. A: Clear barrier, above the water surface. B: Opaque barrier, above the water surface. C: No barrier; control condition.

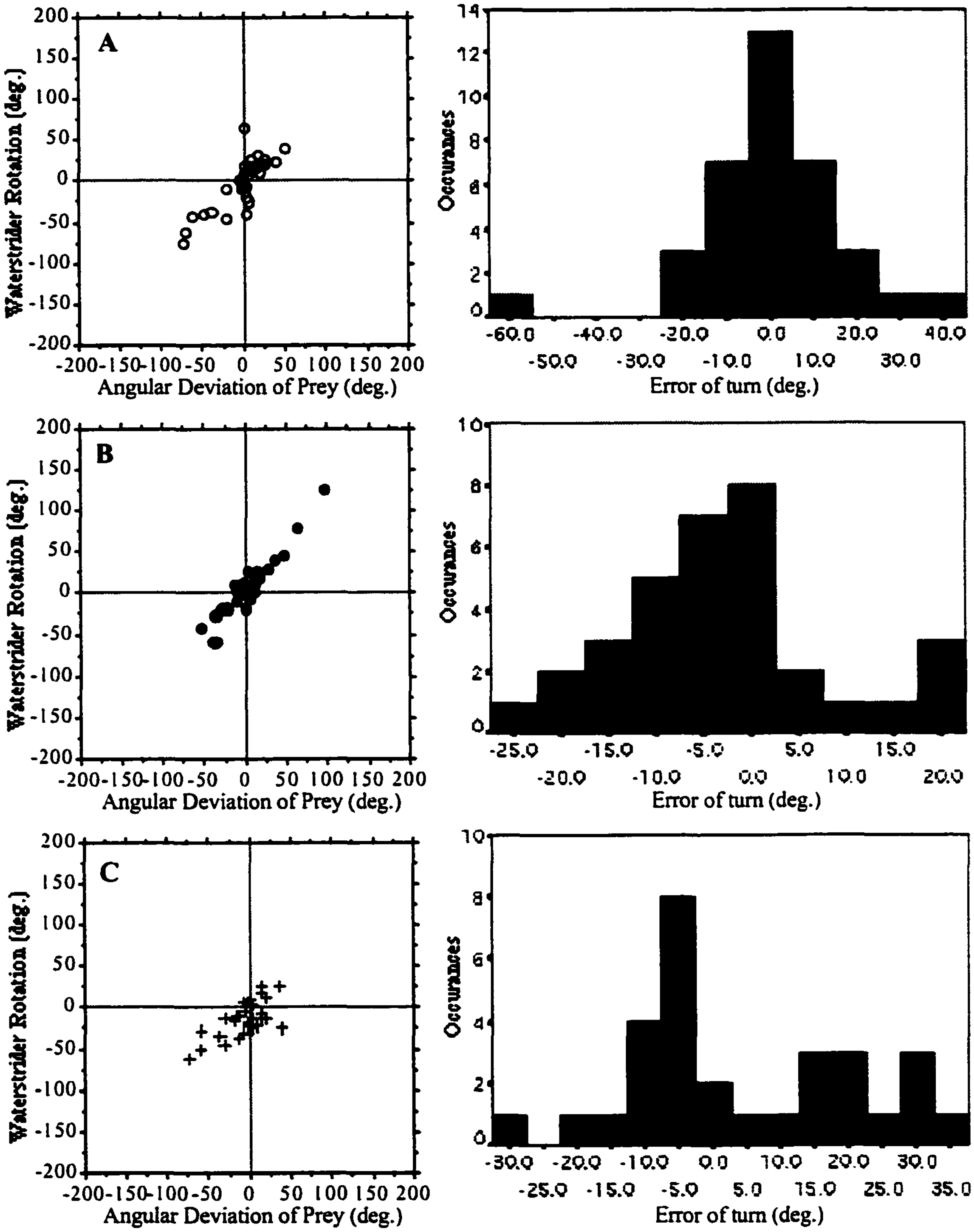


Figure 3-2: Left: Rotational component of waterstriders' second strides, showing angular deviation of prey versus the angle of rotation made by the waterstriders. Right: Accuracy of rotations. Error of turn is a waterstrider's rotation minus the angular deviation of the prey. Positive error indicates over rotation. A: Clear barrier, above the water surface. B: Opaque barrier, above the water surface. C: No barrier; control condition.

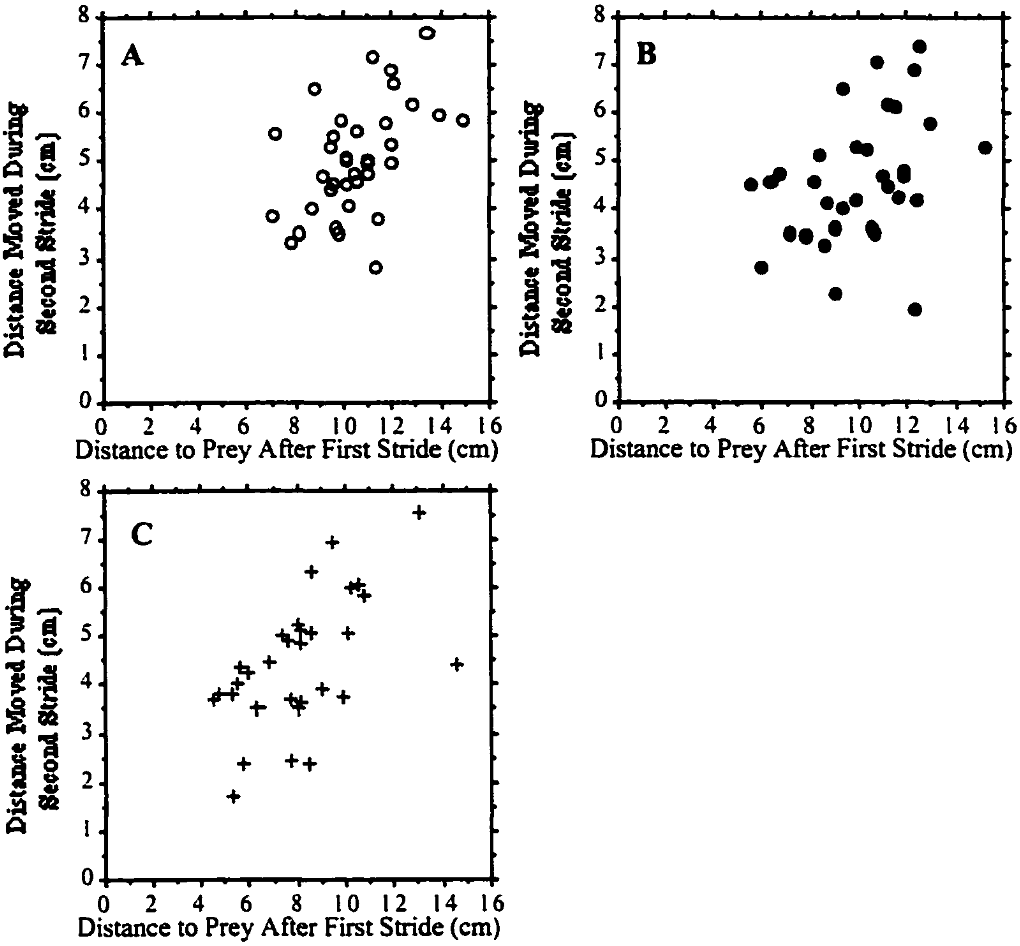


Figure 3-3: Distance between prey and waterstrider after the completion of the first stride plotted against the distance moved by the waterstrider during the second stride. A: Clear barrier, above the water surface. B: Opaque barrier, above the water surface. C: No barrier; control condition.

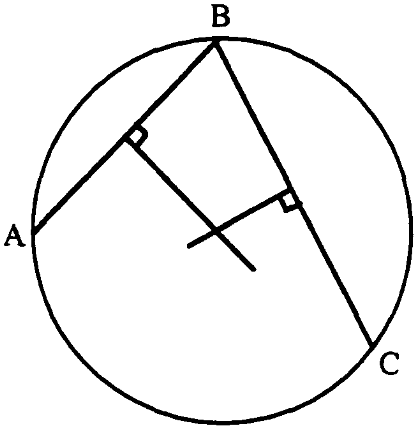


Figure 3-4: The use of two chords to find the centre of a circle. A, B, and C represent three points on the circle. The intersection of the perpendicular bisectors of chords AB and BC identify the centre point of the circle.

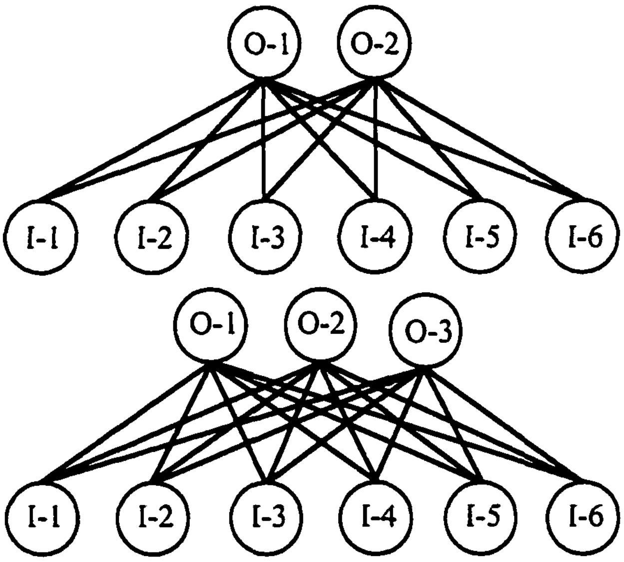


Figure 3-5: The two network type architectures. Top: Network type 1. Bottom: Network type 2. I-1: Right prothoracic receptor, I-2: Right mesothoracic receptor, I-3: Right metathoracic receptor, I-4: Left prothoracic leg, I-5: Left mesothoracic leg, I-6: Left metathoracic leg, O-1: Output unit 1, O-2: Output unit 2, and O-3: Output unit 3.

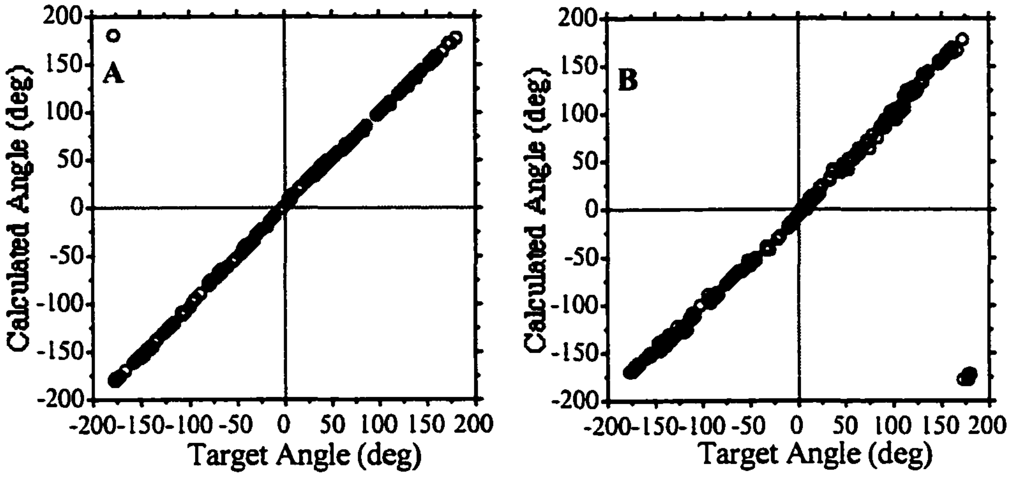


Figure 3-6: Angular calculations for type 1 networks. A: Curvature. B: Amplitude.

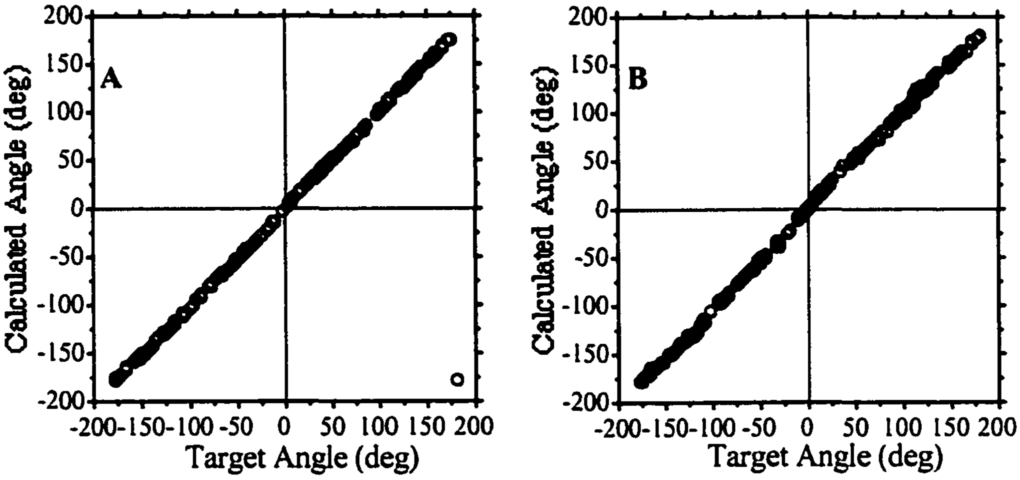


Figure 3-7: Angular calculations for type 2 networks. A: Curvature. B: Amplitude.

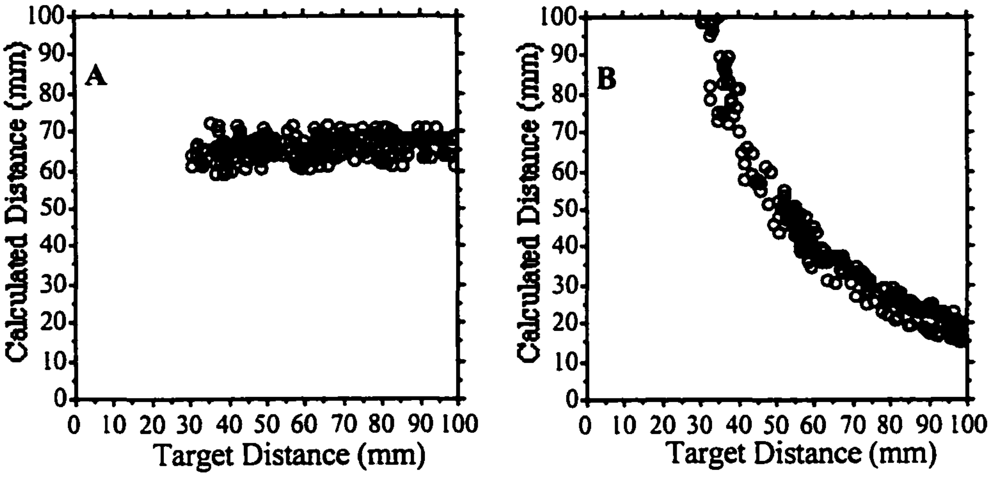


Figure 3-8: Distance calculations for type 1 networks. A: Curvature. B: Amplitude.

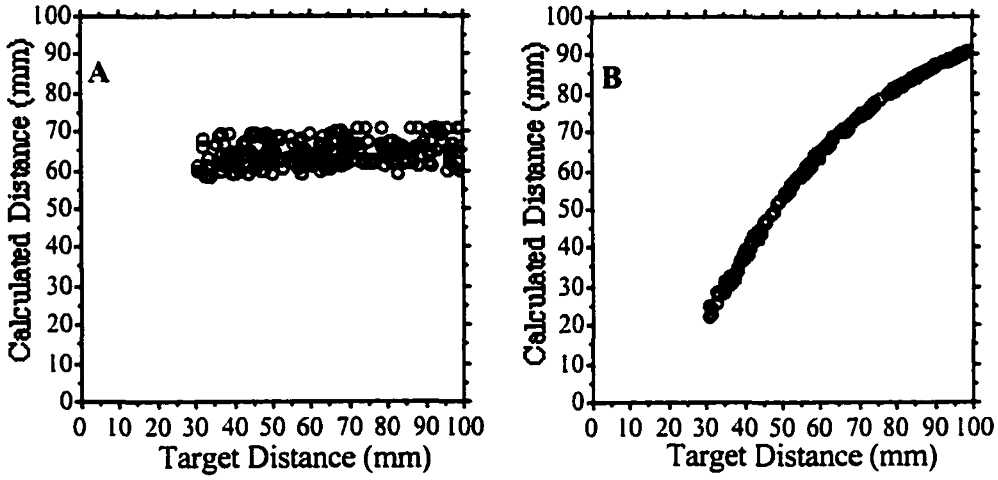


Figure 3-9: Distance calculations for type 2 networks. A: Curvature. B: Amplitude.

Chapter 4:

Waterstriders Hunting Under Non-beacon Homing Conditions

Introduction

The research discussed in the previous two chapters focused on the locomotory behaviour of waterstriders hunting prey items that remained on the surface of the water and producing vibrations during the attack. Thus, the prey served as a beacon source to guide the waterstriders' movement. The work presented in this chapter, however, moves beyond beacon-guided navigation, investigating waterstriders' ability to spatially represent the location of prey items that do not provide homing information.

Given what is known about waterstrider behaviour, is there good reason to believe that they can represent the spatial position of a prey item in memory or are they only capable of finding prey that offers beacon-homing cues? During hunting waterstriders can not be assured of having a constant vibratory signal produced by a prey item to use for guidance. Waterstriders do, in fact, continue to move toward a temporarily non-moving prey item. There are a variety of reasons why prey items may not produce continuous surface vibrations. Crickets, for example, when dropped on the water surface freeze in place for a short period of time (personal observation). Other prey items, such as juvenile waterstriders, have been observed to wait motionless until an attacking adult waterstrider is quite close before attempt an escape by executing a looping path behind the adult (Jamieson & Scudder, 1979). Waterstriders that execute an especially rapid attack in which they do not pause between strides would be incapable of reacquiring vibratory information about the prey's position due to the disruption of surface vibrations caused by their own vigorous movement. Although this suggests that waterstriders should spatially represent the position of their prey in memory, it is also possible that they are simply moving along a pre-activated ballistic course.

Extensive research with other insects, particularly the Hymenoptera (i.e., ants, bees, wasps, and termites), has shown that insects are capable of navigating over short and long distances in the absence of beacons to guide their route. The desert ant *Cataglyphis*, for example, uses a highly accurate form of path integration to guide its return to the nest after long foraging trips (Müller & Wehner, 1988; Schmidt, Collett, Dillier, & Wehner, 1992). Utilizing polarized light (Wehner, 1976; Wehner, 1984) and a simple algorithm for computing turns (Müller & Wehner, 1988) *Cataglyphis* foragers are capable of very accurate navigation. The ant also uses the same system of path integration when searching for the nest opening after being displaced by an experimenter. Over the space of an hour, the ant can walk several hundred meters in ever increasing loops that are re-centred, via the path integration system, at the site of the (now) fictive nest opening (Wehner & Srinivasan, 1981).

Cataglyphis, like other social insects, also engages in piloting, that is, orientation using known landmark features, when returning from foraging trips (e.g., Burkhalter, 1972; Collett, Dillmann, Gieger, & Wehner, 1992; Wehner & Flatt, 1972; Wehner, Michel, & Antonsen, 1996). Similarly, honeybees can use path integration and piloting techniques on foraging trips (e.g., Cartwright & Collett, 1982, 1983; Cheng, 2000; Cheng, Collett, Pickhard, & Wehner, 1987; Collett & Rees, 1997; Dyer, 1991; Menzel, Geiger, Jeorges, Müller, & Chittka, 1998). Interestingly, honeybees are capable of switching between piloting and path integration as the situation demands. For example, Dyer and Gould (1981) showed that bees will utilize landmark references for navigating when clouds block polarized light, and prevent the use of path integration. Although the majority of studies investigating insect navigation focus on foraging there are some exceptions, dealing with, for example, territoriality. These studies show that landmarks are important for delineating territoriality in some of the social insects, such as the cicada killer wasp (Eason, Cobbs, & Trincat, 1999).

Although many other insects are capable of utilizing path integration and/or piloting in non-beacon homing conditions, it is not entirely reasonable to hypothesize similar abilities in hunting waterstriders on this basis. The bulk of the studies with Hymenoptera deal with foraging. While foraging or scavenging in ants, for example, can be seen as a form of predation (e.g., Curio, 1976), it is not of the same form as the hunting behaviour of waterstriders. In addition, ants and bees are central place foragers. That is, they always return to a fixed place, the nest, after their foraging trip. Although some waterstriders are territorial (e.g., Blanckenhorn, 1991; Hayashi, 1985; Jablonski & Wilcox, 1996) and can return to their home range after leaving it (Vepsäläinen & Nummelin, 1985b) this does not make them central place foragers. Hence, while important, the many studies of path integration and piloting during foraging by the social insects do not generate conclusive predictions concerning waterstriders hunting under non-beacon conditions. However, when studies of spatial representation by hunting jumping spiders are also considered, the suggestion that waterstriders can spatially represent prey position in memory appears more justified.

Although jumping spiders are not insects, they share many features with waterstriders. Like waterstriders, jumping spiders are predators that stalk, chase, capture live prey, and hunt individually (e.g., Gardner, 1965). For example, the initial pattern of rotation towards a prey item of jumping spiders, described by Land (1971), is remarkably similar to that of waterstriders, as seen in Murphey (1971b). Jumping spiders have a well developed visual system (e.g., Land, 1969), will lay in wait for prey items to come near, and are not central place foragers. There are, of course, a number of differences, the obvious one being that waterstriders and jumping spiders belonging to different classes. However, with regard to hunting, the most significant differences are that jumping spiders are not restricted to a two dimensional surface as are waterstriders, and jumping spiders use visual, rather than vibratory, stimuli to identify and track prey items.

Interestingly, various species of jumping spider are capable of planning routes to reach a prey item. Hill (1979) tested jumping spiders' (*Phidippus sp.*) ability under naturalistic conditions to reach a prey item suspended near the top of a vertically oriented leafy plant stem. Immediately after a spider, started at the bottom of the plant, initiated its upward pursuit the prey was removed. As a spider moved upwards it periodically reoriented to face the expected location of the prey. Spiders continued their ascent until they reached the former position of the prey item, demonstrating that they were capable of holding the spatial position of a non-visible prey item in memory. Similarly, Tarsitano and Andrew (1999) have shown the jumping spider *Portia labiata* is also able to hold spatial information in memory, planning detours along three-dimensional mazes to reach prey items, and engaging in complex scanning behaviour to plot the best route to the target. *Portia* also uses detours when hunting under natural conditions. For example, *Portia* will maneuver to a position above an orb weaving spider, *Argiope appensa*, secure a silk drag line, and attack the unsuspecting prey from above (Jackson & Wilcox, 1998).

Given these accounts of the social insects' and jumping spiders' spatial representation of targets while foraging, returning to a nest, and hunting, it seems reasonable to hypothesize that waterstriders, although operating under different conditions, may also have the capacity to create spatial representations of their prey's position in non-beacon homing situations. The additional question is now raised as to what information waterstriders might utilize when spatially representing the position of a prey item that is not providing beacon cues. Several possibilities present themselves. First, waterstriders could make use of some form of path integration. While the prey item produces surface vibrations, waterstriders could encode the position of the prey with respect to themselves and, using path integration, plan a route to the prey's location should the vibrations cease. Second, waterstriders could utilize landmarks when representing the prey's location on the water surface. After determining the prey's position from vibratory stimuli waterstriders could represent the prey's location with respect to surrounding landmarks. If the beacon information is stopped waterstriders could then use their position relative to the landmarks to guide their path to the prey. A third option is that some combination of path integration and landmarks are used in hunting.

Given that waterstriders have a well developed visual system used to identify and recognize selected landmarks during drift compensation (e.g., Junger & Dahmen, 1986; Junger, 1991), it is reasonable to hypothesize that visual landmarks could play an important role in guiding their movement towards prey under non-beacon conditions. Path integration, by contrast, could prove more difficult for waterstriders to use. *Gerris remigis*, a stream dwelling waterstrider, is apparently incapable of judging the speed of a current without the use of visual cues (Junger & Varjú, 1990). This means that any form of path integration utilized by waterstriders would require them to use landmarks to continually compensate for drift during movement. Although this could certainly be done, it may inject an extra degree of complexity in the navigation process. Arguing from a parsimonious perspective, it may be less taxing for waterstriders to preferentially rely on piloting when landmarks are available, especially given that they have a well developed place fixing neural system already in place that utilizes landmarks.

The question becomes one of whether or not waterstriders can represent the position of a prey item that is not providing beacon-homing information and whether the presence or absence of landmarks has an affect on any such spatial representation. Presenting a waterstrider with a prey item, allowing the prey to produce surface vibrations, then removing the prey item from the water immediately after the waterstrider initiated its attack was used to test these questions experimentally. Trials were run in the presence or absence of landmarks surrounding the testing arena. Waterstrider locomotion was analyzed to detect differences in movement patterns before and after prey was removed.

Methods

Subjects

Subjects were 20 male and 20 female adult *Gerris remigis* waterstriders collected from Blackmud Creek in Edmonton in May 1999. The waterstriders, separated by sex, were housed communally in groups of 10 in 40x25x15 cm plastic tanks covered with tightly fitting screen lids and filled with 5-8 cm of dechlorinated tap water. Each tank contained several small (approx. 4 cm^2) Styrofoam platforms for the waterstriders to rest on and for females lay eggs upon, and an airstone to provide water circulation. The room in which the tanks were housed was on an 18 hours on, 6 hours off day/night cycle. Light was provided by a row of overhead fluorescent lights. Food, a mixture of dead crickets, houseflies, and fruit flies was added to each tank every three days. When juvenile waterstriders hatched they were removed to a separate tank to prevent adults from consuming them. Once a week the tank water was changed and tanks cleaned.

Houseflies served as prey items in the experiments. The flies were laboratory bred in the Department of Biological Sciences and a fresh supply was continuously available. Between testing days, the flies were housed in a small plastic container kept in a refrigerator to lower their metabolic rate and prolong their life expectancy. They were allowed *ad libum* access to food (a mixture of powdered sugar, powdered milk, and powdered egg) and water. When needed for an experimental trial several flies were transferred to a smaller plastic container and put in an ice bath to render them temporarily immobile. Both wings were clipped off and a fine silk thread (Uni-Products, W 8/0), approximately 30 cm long, affixed to their back using a fast setting cyanoacrylate resin. Typically, at least five flies were prepared in this manner at the same time.

Waterstriders were housed in a testing room on the south side of the fourth floor of the Psychology wing in the Biological Sciences Building on the University of Alberta campus. Room temperature remained relatively stable at about 20°C, although the temperature often rose to about 26°C for several hours on testing days due to the use of incandescent lighting. Humidity was relatively stable at about 50%.

Apparatus

The testing apparatus was located in the same room as the waterstriders' home tanks. The testing arena was a circular barrel made of heavy yellow plastic 60 cm high and 48 cm in diameter at its upper rim. The arena was filled with dechlorinated tap water to 12 cm below its upper rim. The mass of the water in the arena served to dampen vibrations transmitted through the room's floor so that no surface ripples were visually detectable. The water in the arena was changed on a weekly basis and, when not in use, the arena was covered with a thin sheet of plastic to prevent debris from falling onto and contaminating the water surface.

Landmarks consist of 95 cm lengths of 2 cm diameter PVC piping painted gloss black and mounted vertically in small wooden bases. When used, the landmarks were positioned at various angles and distances around the arena, as shown in Figure 4-1.

A black and white video camera was suspended from the ceiling, centred over the arena 150 cm above the water surface. The camera was connected to Panasonic VHS NV-8400 VCR that was wired to a Commodore 1084 black and white monitor. All experimental trials were filmed and recorded with this system. To allow the researcher to determine a fairly precise position of the waterstrider and prey, a grid scaled to represent 2 cm increments in the testing arena, was overlaid on the monitor screen.

To prevent external cues from providing directional information, the entire arrangement of arena and landmarks was surrounded by vinyl shower curtains (coloured light blue), arranged so that they overlapped to prevent gaps, hung on a circular track suspended from the ceiling of the room. To prevent the ceiling from providing directional cues another vinyl shower curtain, with a hole in its centre for the camera lens to project through, was suspended horizontally from the circular track.

Eight 150 W bulbs provide light for the testing arena. The lights are arranged symmetrically, as shown in Figure 4-2. During testing, the room's fluorescent lighting was turned off and the door remained closed. The one window in the room was blocked with heavy black plastic.

Experimental Trials

There were two experimental conditions: landmarks present and landmarks absent. In both conditions a waterstrider was presented with a live prey item which was removed from the water surface immediately after an attack was initiated. In the landmark present condition the landmarks were arranged as shown in Figure 1; the landmarks were removed for the landmark absent condition. Otherwise, the protocol of the trials was identical.

The forty waterstriders were divided into Divisions A and B, each of ten males and ten females. Each Division was further subdivided into Groups 1 and 2, each of five males and five females. The forty waterstriders were randomly selected from a larger population; further subdivisions were also made randomly. Each waterstrider was identified by a small square of white plastic (2x2x0.2 mm) labeled with a distinguishing number glued to the dorsal side of its thorax.

Each waterstrider received 40 test trials, five per day, across eight testing days. All waterstriders within a Division were tested on the same day. On the first day of testing waterstriders from Division A were run. Division B waterstriders were tested on the next day, and so on, until each Division had gone through the eight days of testing. The order of testing of the two groups within each Division was to alternate across days. For Division A the landmark-present condition was to be run first on a testing day, while the landmark-absent condition was always run first for Division B (see Table 4-1). Within Group testing order was determined by the use of a random number table.

Unfortunately, an error was made on the last day of testing for each Division. For Division A the landmark absent condition was run first while for Division B the landmark present condition was run first. In addition, the order of Groups was tested incorrectly on day 7 for Division B with Group 2 being run first rather than second. The consequence of these errors was that for both Divisions Group 1 received 5 exposures to the landmark present condition whereas Group 2 received 5 exposures to the landmark absent condition.

Food was withheld from the waterstriders for two days prior to testing to ensure motivation. After a waterstrider was transferred from its home tank to the arena, it was given five minutes to acclimatize to the new surroundings before test trials were initiated. Each waterstrider was only given six exposures per testing day to a prey item in an effort to prevent the extinguishing of the hunting behaviour to prey items that could never be caught.

As an additional aid to prevent the extinction of hunting behaviour, on the sixth trial of the day a waterstrider received a food item. On this trial a single previously killed cricket was dropped onto the water surface of the arena and the live prey item (a housefly) was positioned next to it. Although the live prey was removed before the waterstrider could capture it, waterstriders accepted the cricket in its stead. Approximately five minutes later, the waterstrider was captured and moved to a temporary holding tank where it could continue feeding. Once all the members of a Group were tested they were returned to their home tank and provided with additional food. Note that only the results of the first five trials are used in analysis.

For testing, the free end of the thread glued to a fly was attached to an alligator clamp on the end of a 100 cm long, stiff wire rod. During trials the experimenter sat outside the curtain and used the rod to place the fly on the water surface of the arena. The rod, from which the fly was suspended, was inserted through a small gap in one side of the curtain, with the gap being closed around the rod, thereby minimizing a waterstrider's view of objects beyond the curtain. The experimenter used the image on the video monitor to adjust the placement of the fly.

Prey was positioned according to a previously generated random distribution. The positions were normally distributed in an annulus centred on the waterstrider. The inner and outer radii of the annulus were 5 and 20 cm, respectively. Individual positions were generated in the following way. An initial X-Y data set that was bivariate normal and uncorrelated (i.e., x_i, y_i, $i=1,\dots,n$) was generated. Then, for $r_i = (x_i^2+y_i^2)^{0.5}$ and $w_i = \mathrm{acos}(x_i/r_i)$, the new coordinates became $x_i' = (r_i+L)\cos(w_i)$ and $y_i' = (r_i+L)\sin(w_i)\sin(y_i)$, where L was the inner radius of the annulus, in this case 5 cm. The grid on the monitor screen was used to position the prey as closely as possible to the designated random position.

A trial was initiated if the waterstrider was not actively moving about the arena, not grooming, and the prey could be placed according to the pre-determined position. This often necessitated waiting until the waterstrider had moved to a place in the testing arena that allowed for the proper placement of the prey. When this was achieved the prey item was lowered onto the water surface where it remained either for ten seconds or until the waterstrider initiated a directed (i.e., hunting) movement towards it. In the event of a directed movement, the prey was removed from the water as soon as possible after the hunting response was initiated and the rod and prey moved below the outside rim of the arena, out of sight of the waterstrider. A trial was deemed ended by one of four occurrences: 1) the waterstrider remained motionless for ten seconds, 2) the waterstrider began grooming, 3) the waterstrider came in contact with the wall of the arena, or 4) sixty seconds had elapsed since the waterstrider initiated a movement towards the prey item. Once a trial ended, at least sixty seconds were allowed to elapse before the initiation of another trial. All trials were video taped for subsequent analysis. The experimenter noted additional comments and behavioural observations.

Prey items were alternated after every waterstrider. The same fly was used for all 6 trials a waterstrider received each day. When not in use, the flies were suspended in open space from their threads. New flies were prepared each testing day.

Video Analysis

Experimental trials were recorded to VHS tapes. Tapes were played back through a Sanyo VHR-9426A VCR connected to a Macintosh G3 Powerbook through a CapSure™ PCMCIA video card (Par Technologies, Inc.). Experimental trials recorded to tape were stepped through frame by frame using Apple MoviePlayer. Important individual frames (initial placement of prey item with respect to the waterstrider, start and finish positions of strides made by the waterstrider during a trial) were copied and saved as TIFF files using the program Graphics Converter 2.0. Once in TIFF format, the images could be read by NIH Image, an image analysis program. Using NIH Image, X and Y coordinates of prey and waterstrider position were recorded and saved as text files for subsequent statistical analysis and interpretation.

During the analysis of video images, a decision was made as to whether or not the waterstrider was operating under beacon homing or non-beacon homing conditions. When the prey item was in contact with the water surface, thereby producing surface vibrations, the waterstrider was classified as operating under homing conditions. Strides made after the prey was removed from the surface were described as being made under non-homing conditions. Surface waves produced by the prey were generally fairly visible on the videotape. Multiple observations suggested that, based on the apparent rate of wave propagation, if a waterstrider was within 10 cm of the prey it would take six frames (0.2 seconds) for the surface waves made by the prey to pass the waterstrider after the prey was removed. When the prey was between 10-20 cm away from the prey, twelve frames were required to elapse between the time the prey was removed and a stride was initiated for the stride to be classified as non-homing. Sufficient TIFF files were captured to account for at least one non-homing strides for each trial in which non-homing strides were observed.

Results

General Introduction to Shape Analysis

Statistical shape analysis (SSA) allows for a unified statistical analysis of direction and distance through the comparison of areas, a potential advantage when evaluating movement patterns. I used Kendall planar and Kendall spherical coordinates in the analysis of stride shapes made by waterstriders under the presence and absence of landmarks.

For each stride, a triad of three planar coordinates was recorded: waterstrider start (S) and finish (E) positions and prey position (P). The planar coordinates of each point (i.e., of S, P, and E) specify a triangular configuration. It is the resultant triangular shapes that are analyzed using SSA. Each triangular configuration can be transformed into a single datum by using one of several coordinates systems (e.g., Bookstein, Kendall). This procedure maps a configuration such as that depicted in Figure 4-3 into a spherical geometry. Different triad configurations are located at different parts of the sphere. For example, if the three points of a triad are collinear, then the resulting spherical coordinates will fall along the great circle of the sphere that passes through the poles. Note that triads will only correspond to the same point on the sphere if they share the same shape. The shape of a triad is invariant when the triad is translated, rescaled, or rotated (Stoyan, Kendall, & Mecke, 1995, p. 257).

A coordinate system is necessary for describing the shape of the triads. As mentioned above, the shape of a triad must be invariant, so the chosen coordinate system must retain a triad's shape under translations, scaling, and rotation. For this study, the triads consist of $k = 3$ points in $m = 2$ dimensions. The challenge becomes one of standardizing the triads to generate useful comparisons. Bookstein planar coordinates, for example, remove the similarity transformation by translating, rotating, and rescaling configurations so that points one and two of a triad are set to fixed positions. The baseline points are set at (-0.5,0) and (0.5,0) (Bookstein, 1984). Bookstein coordinates are straightforward and easy to apply. However, due to a lack of symmetry in choosing the baseline and because correlations can be induced into the coordinates, sometimes different coordinate systems are preferable (Dryden & Mardia, 1998).

I opted to use Kendall coordinates to define the triad configurations. Kendall coordinates are similar to Bookstein coordinates, but location is removed in a different way, using the Helmeret sub-matrix (see Dryden & Mardia, 1998, pp. 34-35 for details). Points one and two of a triad are transformed to $(-1/\sqrt{3},0)$ and $(1/\sqrt{3},0)$, and are referred to as Kendall planar coordinates. As mentioned above, triads can also be mapped onto a spherical space. In doing so, the resultant Kendall spherical coordinates have a shape space that is a sphere with a radius of 0.5, and are defined using polar coordinates (see Figure 4-4 for details on polar coordinates). Coordinates are given in terms of latitude, or more specifically in this case colatitude, and longitude (i.e., (θ, ϕ) for colatitude and longitude, respectively). Figure 4-5 shows a representation of the measure of colatitude and longitude from a triad.

The spherical shape space is partitioned into 6 lunes and 12 half-lunes. By analogy, a lune can be visualized by cutting an orange into six equal pieces, slicing through the poles. Half-lunes would then be formed as cutting each lune in half, along the equator of the orange. Using Kendall coordinates, within each lune, triads forming equilateral triangles are positioned as points at the poles, collinear (i.e., flat) triangles at the equator, and isosceles triangles on the meridians (Dryden & Mardia, 1998).

Movement patterns of waterstriders can be evaluated using the Kendall coordinate system. For example, if waterstriders orient and jump towards the prey then the Kendall points should be clustered along the collinearity meridian. This tendency can be evaluated quantitatively by looking at the geodesic distance of these points from the great circle of collinearity.

Waterstrider Positions used in Analysis

I analyzed three sets of strides with shape analysis. As described above, for each trial a stride triad was defined by a waterstrider's starting and ending points and the position of the prey. I defined the stride made by a waterstrider immediately before the prey was removed from the water surface as stride 0 and the first stride made after the prey was removed as stride 1. Only trials for which waterstriders completed both strides 0 and 1 without contacting the prey or touching a wall were used in the analysis. A third stride, designated stride 0-1, was also defined. The three points of stride 0-1 are represented by the initial position of a waterstrider from stride 0 and the ending position of a waterstrider from stride 1 and the position of the prey (see Figure 4-6). Thus, stride 0-1 encompasses the overall movement of the waterstrider over stride 0 and 1 for each trial.

Movement patterns were analyzed for the two landmark conditions, absent and present. Individual waterstriders' trials were grouped across days by condition. Within each landmark condition data from male and female waterstriders were combined.

Shape Analysis

As mentioned above, the geodesic distance of the points representing triads mapped onto spherical space can be evaluated in terms of their geodesic distance from the great circle of collinearity. These distances are represented by the value Z. When Z values are depicted graphically as histograms, a quick and relatively straightforward method of evaluating the accuracy of waterstriders' strides towards the prey position results. If waterstriders move randomly with respect to the prey, one would expect a rectangular distribution across the histogram (i.e., the histogram would be flat). If waterstriders move towards the prey, the distribution of the histogram should be centred on zero.

Figure 4-7 shows the distributions of distances of points from the meridian of collinearity for strides 0 and 1 for the landmark absent and present conditions. It is evident that most trials show shapes that are close to collinear, that is, are directed towards the prey. For stride 0 the landmark absent and present conditions showed values of M = 0.00, SD = 0.33 and M = 0.02, SD = 0.34, respectively. For stride 1 values of M = 0.02, SD = 0.47 and M = 0.02, SD = 0.46 were found for the landmark absent and present conditions, respectively.

Z scores, the geodesic distance of stride shape from collinearity, for strides 0 and strides 1 were analyzed by ANOVA. Landmark absent and landmark present conditions were compared for strides 0 and 1. For both strides no statistical differences were found between the two landmark conditions (for stride 0, $F = 1.24$, $df = 1, 1032$, $p > 0.26$ and for stride 1, $F = 0.008$, $df = 1, 920$, $p > 0.93$). This indicates that waterstriders moved towards the prey under both landmark conditions on both homing and non-homing strides.

While Z scores are easily generated and a good starting point, they only provide basic information about the shape of strides and are not a particularly strong form of analysis. More information is available for analysis when stride shape is represented not simply as a Z value, but in terms of the colatitude and longitude of a triad's shape point with a spherical coordinate system. Within the Kendall spherical coordinate system that I employed, a stride would precisely intersect the prey's position at coordinates 1.05 radians colatitude and 3.14 radians longitude (i.e., 60° colatitude and 180° longitude).

For this shape analysis I used a test of common median direction of two or more distributions, described in Fisher, Lewis, and Embleton (1987), with the assumption that the distributions are the same except for their median directions (see Appendix for details). Because tests of spherical means require rotational symmetry of the distributions tested, I opted to utilize spherical medians instead. Nevertheless, tests of the spherical median are quite robust, sharing properties analogous to those of the linear median.

For each sample (i.e., trial) the deviation of the colatitude and longitude (i.e., (θ,ϕ)) from the pooled sample median was obtained by rotating the sample to the pole described by the median. The deviation of (θ,ϕ) from the pole was then determined and the test statistic Z^2 calculated (see Appendix for details). Z^2 was evaluated against χ^2 criteria with $2r - 2 = 2$ degrees of freedom. Note that the sample spherical median is an estimate of the spherical median. If $\mathbf{X}$ is a vector from the population and $\mathbf{a}$ a randomly chosen direction, then the spherical median is the direction $\mathbf{a}$ for which the average value of θ_a is a minimum (Fisher, Lewis, & Embleton, 1987, p. 111).

Using this test, waterstrider strides under the landmark absent and landmark present conditions were further analyzed. For this analysis reflected coordinates (i.e., the left/right side was eliminated, similar to an "absolute error" measure) were used. Figure 4-8 shows the reflected coordinates for strides 0-1, 0, and 1 for landmark absent and present conditions. The plots use Bookstein coordinates for display purposes. For Bookstein coordinates the baseline points on the triad (waterstrider start position and prey position) are transformed to fit a unit measure of 1.0. With the start position of triads set at the origin the adjusted prey position falls at (-1,0). Each point on a graph represents a single triad.

Stride 0-1 and stride 1 trials for which a waterstrider touched the prey, touched the arena wall, or made two beacon homing strides before the prey was removed from the water surface were not used in the analysis. In addition, for stride 1 there were three cases where the start of the stride coincided with the former position of the target. Because the shape analysis can not interpret a triad in which the two baseline points are at the same position in space, these trials (two in the absent condition and one in the present condition) were excluded from the analysis.

The first test evaluated the combined movement of the waterstriders for stride 0-1 shapes. The landmark absent trials (n = 473) had a median colatitude of 1.38 radians and a median longitude of 2.82 radians. The landmark present trials (n = 447) had a median colatitude of 1.23 radians and a median longitude of 2.87 radians. Waterstriders overshoot the target on both conditions, but there is less of an overshoot under the landmark present condition. Also, the landmark present group is more directed towards the target (i.e., longitude of 3.1415 radians). Evaluated against a chi-square (df=2), the null hypothesis that both conditions have a common median direction can be rejected at the 0.025 level (Z^2 = 8.68).

For stride 0 (beacon homing), the landmark absent trials (n = 473) had a median shape of colatitude = 0.45 radians, longitude = 2.50 radians whereas the landmark present trials (n = 447) had a median shape with colatitude = 0.41 radians and longitude = 2.41 radians. The null hypothesis that both conditions have a common median shape can not be rejected (Z^2 = 1.19).

For the stride 1 (i.e., non-beacon homing) data, the landmark absent trials (n = 471) had a median colatitude of 1.92 radians, median longitude of 2.30 radians and the landmark present trials (n = 446) had a median colatitude of 1.69 radians, median longitude of 2.48 radians. This indicates that waterstriders under the landmark present condition overshoot the target by less of a distance and are more directed towards the target. This difference in the presence versus absence of landmarks was significant, $p < 0.025$ ($Z^2 = 7.69$).

Discussion

The dual purpose of this experimental design was to determine if a waterstrider could continue to navigate successfully towards the prey position under non-beacon homing conditions and whether or not the presence or absence of a landmark array would have an effect on such navigation. The shape analysis interpretation of the data indicates that waterstriders do continue to move towards the prey after the cessation of vibratory signals from the prey, but that their movement is more accurate in the presence of landmarks. More specifically, in the absence of beacon cues and landmarks, waterstriders tend to overshoot the target by a greater distance and are less directed towards the prey position than when a landmark array is available.

It is important to recognize that waterstriders are capable of moving towards the prey position in the absence of landmarks, as shown by the analysis of the geodesic distance of stride shape from collinearity, at least for the first stride after beacon cues have stopped. Whether their accuracy would continue to decline over subsequent strides is an issue for further analysis. Unreported observations from this experiment indicate that waterstriders will make more than one non-beacon homing stride towards the vicinity of a prey item in the absence and presence of landmarks. There would appear to be two possible mechanisms that waterstriders could employ in the absence of beacon cues and landmarks. First, they could utilize an egocentric coordinate system to represent the position of the prey item. That is, instead of representing prey position with respect to landmarks, they would specify the prey position in terms of angles and distances from their own position. This would then necessitate the use of some form of path integration system to guide subsequent movement towards the prey position.

An alternate approach, which would only be appropriate for the first stride after the loss of beacon-homing information, would be for a waterstrider to move for some arbitrary distance in the direction it is pointing at the end of stride 0. Of course, if this technique were employed there would be a significant decrease in accuracy over subsequent strides. Given the results of the collinearity interpretation, it is unlikely that waterstriders employ this second technique. Similarly, while there is a decrease in accuracy when moving towards the prey in the absence of landmarks compared to the presence of landmarks the error levels do not appear large enough to support this second approach. Rather, it is more likely that waterstriders make use of some form of egocentric representation when moving towards a prey item that is not providing vibratory cues in the absence of visible landmarks. The future analysis of subsequent strides (e.g., stride 2 to stride 5) may reveal more details for the interpretation of the form of representation used by waterstriders under this condition.

The implication of the finding that waterstriders are more accurate in their movement towards the prey position in the presence versus absence of landmarks is that waterstriders represent the position of the prey with respect to available landmarks while beacon cues are available to them. When the beacon-guiding vibrations produced by the prey cease, waterstriders utilize their representation of prey position with respect to the landmark array to guide their movement. This indicates that waterstriders continually update their representation of prey position relative to landmarks when they do not require the information, that is, when beacon cues are available. Given that *Gerris remigis* continually tracks the position of a landmark array when on moving water for drift compensation, it is not surprising that they should also encode prey position relative to landmarks. This raises the interesting question of whether the elements of waterstriders' central nervous system involved in drift compensation are also involved in the spatial representation of other environmental features, including prey items, other waterstriders, and predators.

It is, however, also apparent that with the availability of beacon-homing cues the presence or absence of landmarks does not affect waterstrider accuracy when moving towards the prey. This suggests that waterstriders utilize a hierarchy of cues during hunting to guide movement. In the presence of vibratory cues, waterstriders appear to use them. If vibratory information ceases, waterstriders will attempt to utilize a spatial representation of prey position with respect to available landmarks. Finally, should landmarks be unavailable waterstriders may make use of some form of egocentrically represented path integration system. Of course, under natural conditions it would be extremely rare for waterstriders to operate without the availability of landmarks. The only situation that readily comes to mind would be that of waterstriders moving in the dark. Typically, waterstriders retreat to the shoreline, anchoring themselves to vegetation, rocks, or the like, at night. However, one could hypothesize a situation, such as a predatory attack upon a waterstrider after dark, in which a waterstrider would be forced to move in the absence of visual landmark cues.

Given the results from this study, it is apparent that the lack of landmarks under non-beacon homing conditions adversely effects waterstrider accuracy when moving toward the prey position. There are two plausible explanations for how waterstriders utilize landmarks in guiding their navigation. The first is that waterstriders rely on true piloting, that is, the use of landmarks directs their movement. The second, is that they rely on path integration, using landmarks for calibrational information, thereby correcting for positional errors that occur during a stride.

Using piloting, waterstriders would encode the position of the prey relative to an array of landmarks, representing prey location geocentrically. When beacon cues are available, waterstriders could preferentially make use of this information to guide their strides, at the same time representing their own and the prey's position in relation to the landmarks. If beacon cues cease, these spatial representations would be used to direct subsequent strides towards the prey's position. The absence of landmarks would prevent waterstriders from encoding spatial representations, thereby resulting in errors in movement under non-beacon homing.

Under the piloting hypothesis the combining of spatial information might occur as follows. A waterstrider detects a prey item through its tibial-tarsal vibration receptors and converts the angular and distance information about the prey's position into egocentric coordinates. That is, the waterstrider represents the prey's position relative to itself. This information is then used to determine the rotational and translational components necessary for a stride towards the prey. At the same time, the waterstrider has been maintaining a representation of an array of nearby landmarks, perhaps for drift compensation purposes. The position of the prey derived from the vibrations is now placed into the spatial framework of the landmarks. While the vibratory beacon source is available the waterstrider can continue to determine stride rotations and translations from the egocentric representation. However, if the situation should change to one of non-beacon homing then the waterstrider can continue its attack using the representation of the prey's position relative to the landmarks.

Alternatively, waterstriders could rely strictly on egocentric spatial representations using path integration, but only if, as discussed in Chapter 1, landmarks are used to take re-positioning fixes after each stride. Without correcting for errors in movement using re-positioning fixes from landmarks, errors will accumulate in any path integration system. If waterstriders use landmark arrays to calibrate their position after movement then they could encode the location of the prey completely within an egocentric system and still maintain a high degree of rotational and translational accuracy across strides. Thus, path integration could be used to determine the prey position in the absence of beacon cues and help the waterstrider calibrate the direction and distance for a stride. Unlike the piloting explanation, if landmarks are used to calibrate strides controlled by an egocentric path integration system, spatial relations between prey position and landmarks would not need to be encoded.

In this case, a waterstrider could represent the position of a prey item in the following manner. As with the piloting explanation, the information from the vibration receptors is used to represent the prey's position egocentrically. The waterstrider determines the rotational and translational components and makes its first stride towards the prey. Meanwhile, the waterstrider has also been representing its own position relative to an array of landmarks. After completing the stride the waterstrider compares its expected position (determined before the stride was initiated) with its actual position relative to the landmark array. Thus, the landmarks allow the waterstrider to re-position itself, thereby correcting for any positional errors that might have occurred during the stride. As long as the beacon cues are available, such calibration is not especially important, as the vibratory cues can again be used to form an egocentric representation of the prey position relative to the waterstrider. However, should the beacon cues cease, then the representation of prey position relative to the waterstrider's position can still be used to guide locomotion. Now, the use of the landmark array for the comparison of expected to actual position after a stride is executed serves to re-calibrate the waterstrider's position, allowing more accurate movement over subsequent strides.

In the case of both the piloting and path integration with positional calibration hypotheses, in the absence of both beacon cues and landmark arrays the waterstrider is assumed to default to using a path integration system to guide its strides. However, errors will accumulate under this system as the waterstrider will have no means of identifying where, precisely, in the environment it is after each stride. Thus, small errors in locomotion will accumulate across strides resulting in the waterstrider gradually moving further away from the prey's initially encoded position. Unfortunately, it is very difficult to determine whether the piloting or path integration wtih positional calibration hypotheses is correct. Although the piloting explanation is appealing due to its similarity of spatial representation relative to landmark arrays during drift compensation, the alternative path integration explanation can not be ruled out.

Finally, this study demonstrates that shape analysis can be effectively applied to the study of movement patterns. This is a novel application of the statistical technique. Although shape analysis has been used for other biological analysis, such as the comparison of vertebrae and skull shape (e.g., Mardia & Dryden, 1989; O'Higgins & Dryden, 1993), I am unaware of previous applications of shape analysis to the study of movement, spatial representation, or other behavioural questions. Using shape analysis for resolving comparisons of movement patterns has the advantage of allowing one to treat the movement as a cohesive whole instead of needing to separate an organism's movement into constituent components of distance and angles. While I recognize that there are times in which this sort of reductionism is very useful, such as when investigating whether animals encode distance and direction separately, I feel that being able to examine movement as a whole may have certain interesting applications. In fact, as can be seen from the results depicted in Figure 4-8 it is still possible to extract details about distance and direction from the shape analysis protocol, while at the same time analyzing for overall differences in movement pattern across conditions.

	Day 1	Day 2
Division A	G1LP, G2LA	G2LP, G1LA
Division B	G1LA, G2LP	G2LA, G1LP

Table 4-1: Order of testing of waterstriders for the first two testing days for each Division. The following six days of testing follow the same pattern (see text). G1 and G2 represent Groups 1 and 2, respectively. LP and LA represent the landmark-present and landmark-absent conditions, respectively.

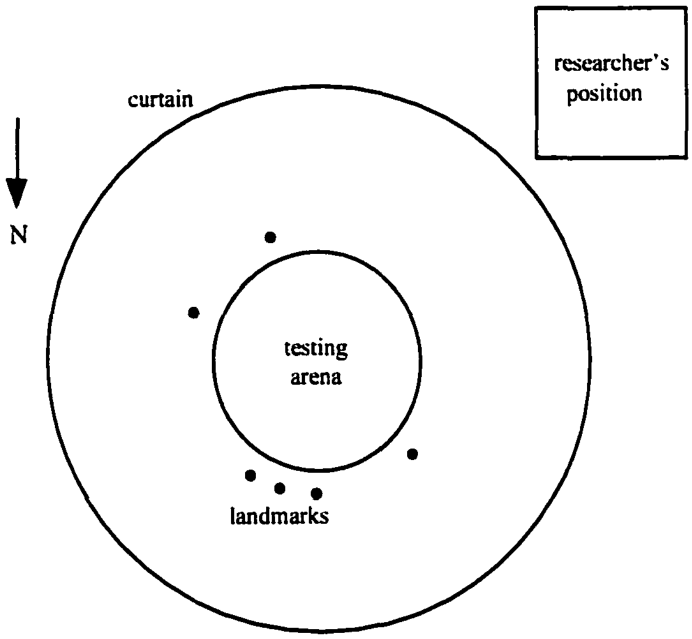


Figure 4-1: Schematic of the testing enclosure, to scale. Diameter of curtain and testing arena, 144 and 48 cm, respectively. Position of landmarks, 2 cm in diameter, for landmark-present condition shown.

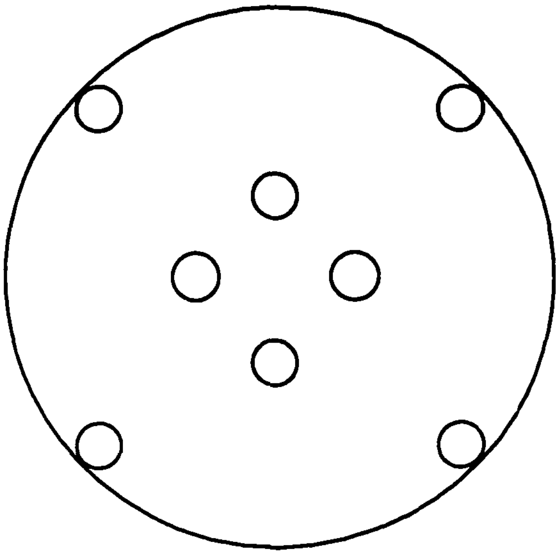


Figure 4-2: Schematic of the placement of the lights, to scale. The large circle represents the curtain; small circles depict the individual 150W lights. The four outer lights are mounted on the metal rods, dropped from the ceiling, that support the circular track for the curtain. The four inner lights are mounted from the ceiling itself.

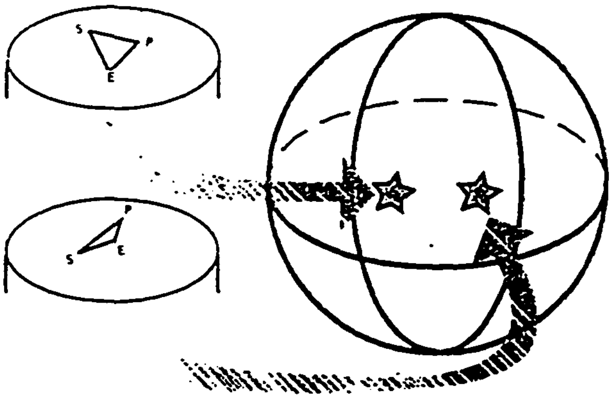


Figure 4-3: The configuration of the start (S), the finish (E), and the prey (P) of the trial's stride are translated into coordinates giving a location on the surface of a sphere.

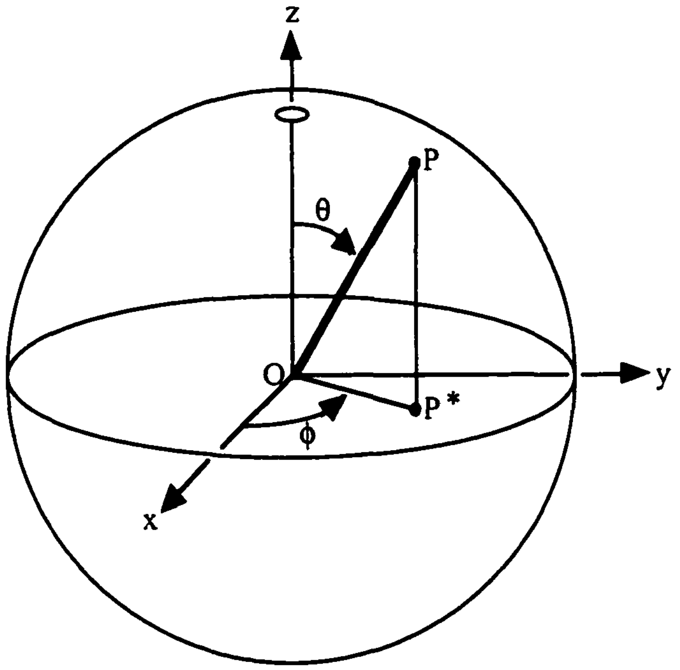


Figure 4-4: Polar coordinates for a sphere of unit radius centred at O. Three orthogonal axes (x,y,z) are shown. P, a point on its surface is identified by the vector OP. θ, the angle between OP and Oz, is the *colatitude*. ϕ, the angle measured anticlockwise between Ox and OP* (the projection of OP onto the x-y plane), is the *longitude*. Therefore, $0° \leq \theta \leq 180°$ and $0° \leq \phi \leq 360°$. The coordinates of P, in terms of x, y, and z, are $x = \sin\theta \cos\phi$, $y = \sin\theta \sin\phi$, $z = \cos\theta$. Adapted from Fisher, Lewis, & Embleton (1987), p. 18.

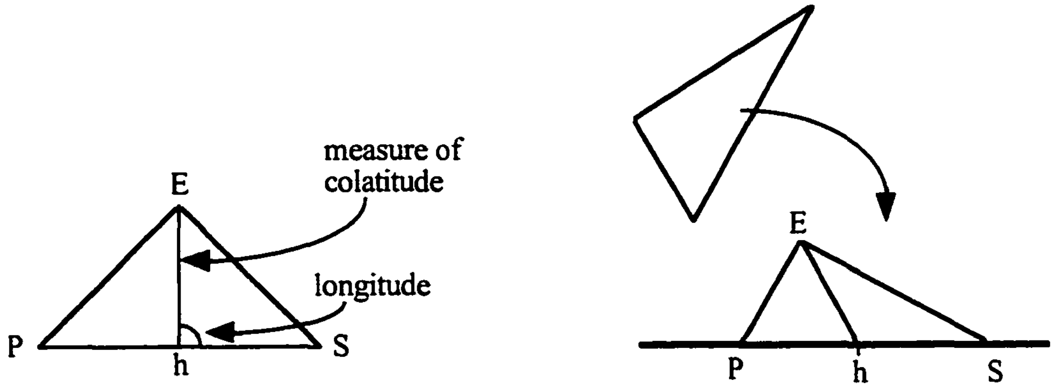


Figure 4-5: Left: Measures of colatitude and longitude from a triad. The ray from the centre of the baseline to the vertex provides a measure of colatitude. Specifically, this length is $\sqrt{3}\left(\tan(\frac{\text{colatitude}}{2})\right)$. Right: Rotation of triad to place it on the appropriate baseline of the coordinate system. Note that colatitude and longitude are measured from the halfway point (h) between the two baseline points (i.e., S and P) to the third point of the triad configuration (i.e., E). S = waterstrider starting position, E = waterstrider ending position, P = prey position, h = midpoint between S and P.

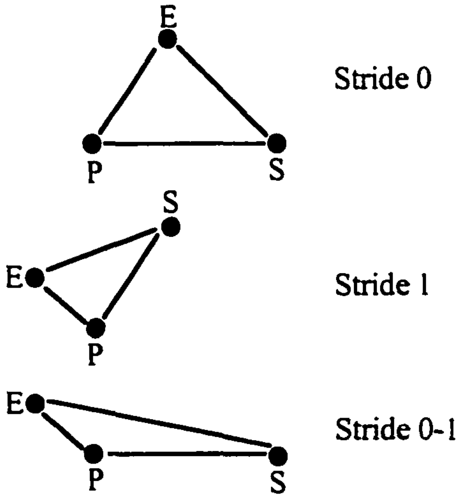
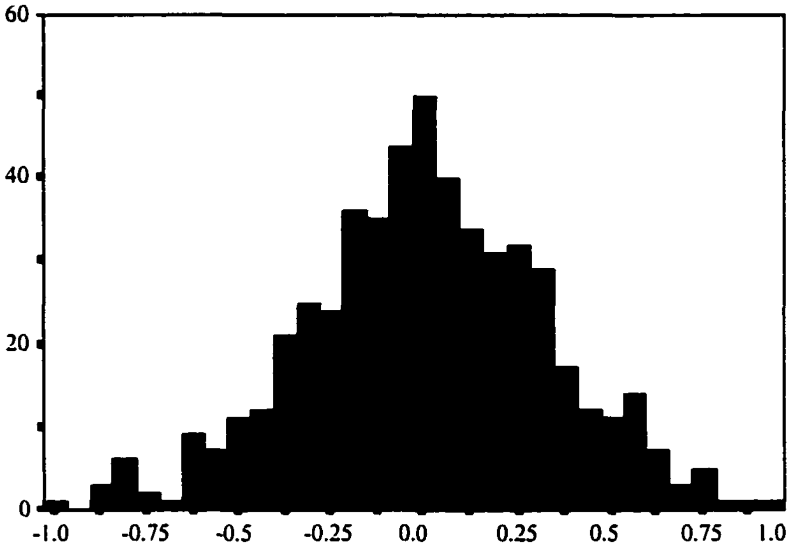
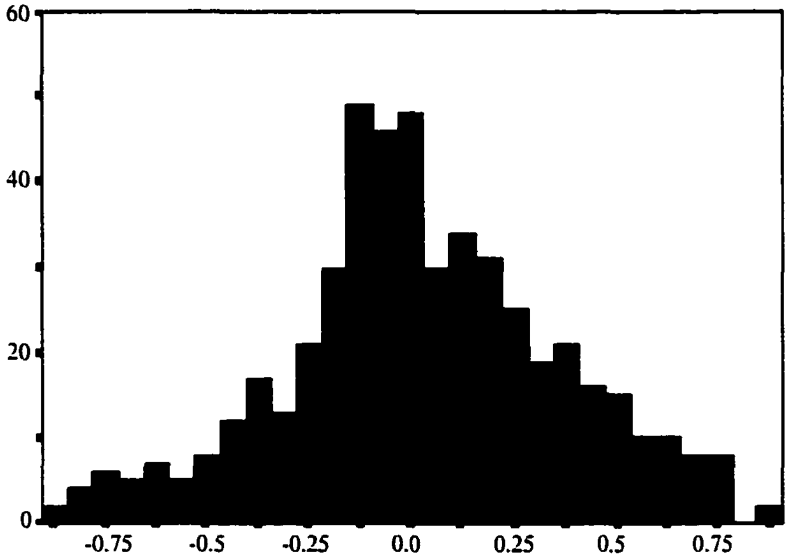


Figure 4-6: Representation of stride 0, stride 1, and stride 0-1 for a single trial. S = starting position of waterstrider, E = ending position of waterstrider, P = prey position. The lines connecting the points depict the shape formed by each triad.

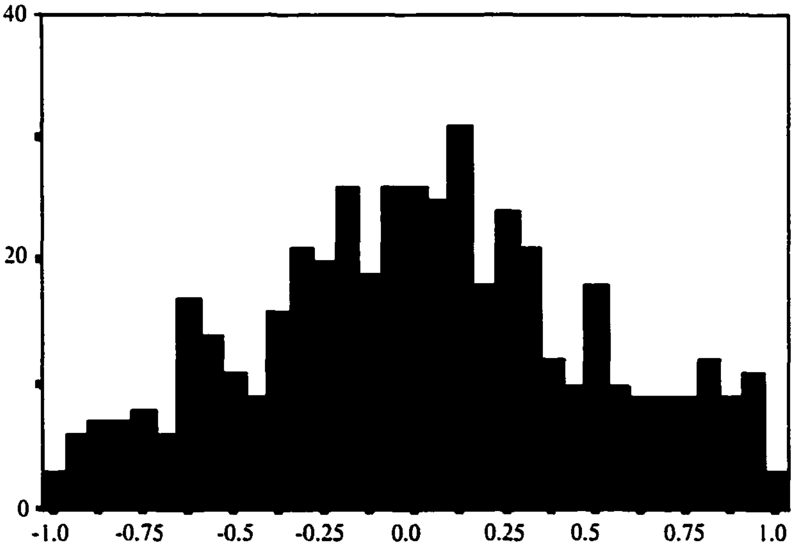
A. Stride 0, Landmark Absent



B. Stride 0, Landmark Present



C. Stride 1, Landmark Absent



D. Stride 1, Landmark Present

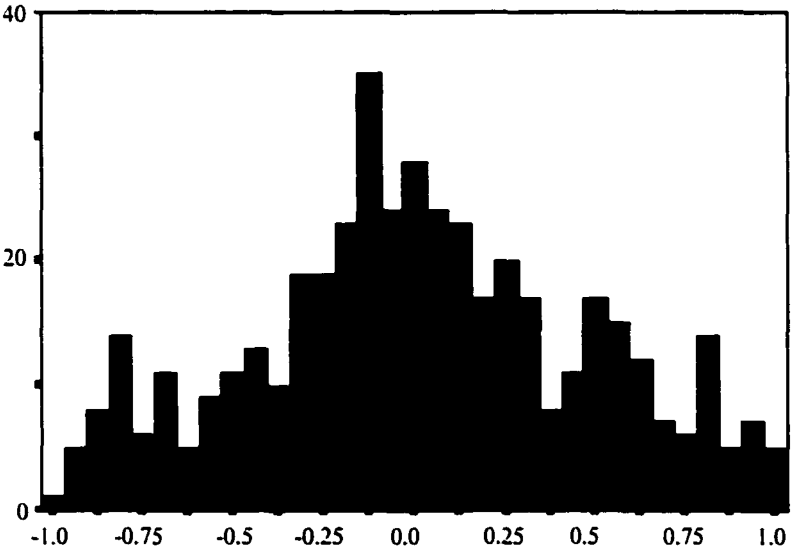


Figure 4-7: Rectangular distributions of Z, the geodesic distance from the meridian of collinearity.

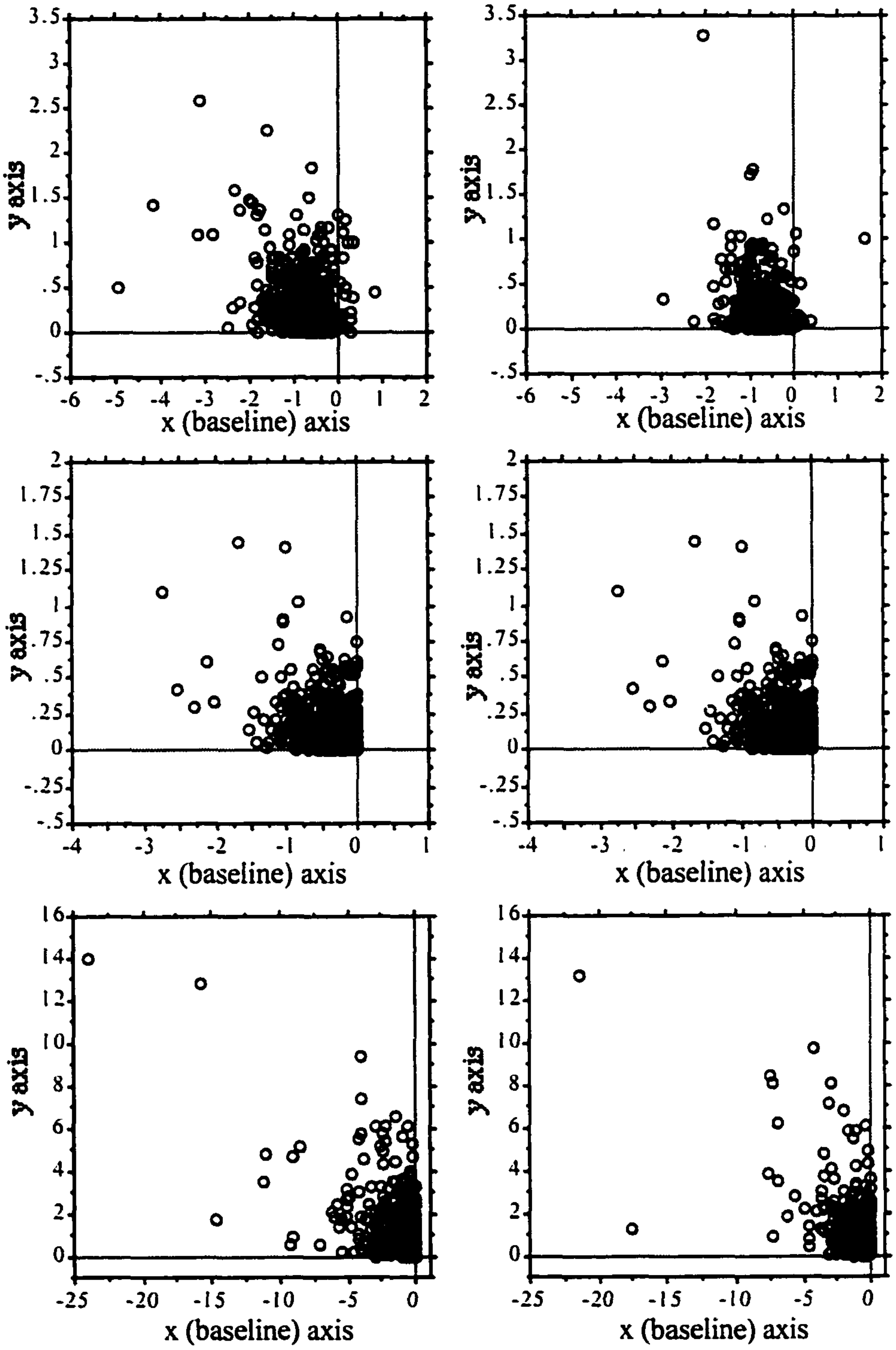


Figure 4-8: Plots of triads in Bookstein coordinates. With Bookstein coordinates the baseline points of each triad are transformed to a unit length of 1.0. The starting position of a stride is set to (0,0) and the prey position is at (-1,0). Note that all triads are plotted with reflected coordinates. The landmark absent condition is shown on the left and the landmark present condition on the right. Top: Stride 0-1. Middle: Stride 0. Bottom: Stride 1.

Chapter 5

Conclusion

My research has investigated the spatial representation of waterstriders engaged in the act of hunting live prey. I have shown that a waterstrider can use sensory input from a prey item to identify the presence of prey and guide it to the prey's position. This constitutes a condition of navigating under beacon homing conditions, that is, stimuli produced by the prey inform the waterstrider of its position in the environment. It seems likely that vibratory cues are most significant for a hunting waterstrider. In cases in which the prey is not visibly obscured but vibratory cues have been blocked, waterstriders do not initiate attacks on the prey. Similarly, when vibrations produced by the prey are permitted to reach a waterstrider even though the prey's position is not visually apparent, an attack towards the prey is initiated. I have also demonstrated that waterstriders can successfully represent the position of a prey item after it has stopped producing beacon homing cues. Further, in such instances waterstriders will make use of landmark arrays to guide their movements towards the prey's position. In the absence of landmarks under non-beacon homing waterstriders will still move towards the prey position, albeit not with the same level of accuracy as when landmarks are available. This suggests that waterstriders also have a path integration system that they can use when hunting. Although not explicitly investigated, by comparing the findings of the several studies I reviewed in this document, I suggest that when hunting waterstriders rely on a hierarchy of strategies to identify, localize, and intercept a prey item. I propose that waterstriders preferentially use vibratory stimuli produced by the prey as a beacon to guide an attack. However, at the same time waterstriders spatially represent the position of the prey with respect to available landmarks. If the beacon cues cease, waterstriders shift to using piloting or path integration (with landmark calibration) information to continue the attack. Finally, in the event that under non-beacon homing conditions landmarks are unavailable, waterstriders can still carry out the attack, at least in the short term, presumably by relying on an uncalibrated path integration system.

While a new finding, my demonstration of the role of landmarks in representing prey position in hunting corresponds well with previous studies that have shown waterstriders to maintain territories, leave and return to specific locations, and maintain a fixed position on streams. Based on his study of their drift compensation mechanism Junger (1991) proposed that waterstriders possess a memory for landmark arrays similar to other insects because they could return to a preferred place on the edge of an artificial canal after an excursion. Although dealing with hunting rather than drift compensation behaviour the results of my study described in chapter four provide additional evidence in support of waterstriders utilizing landmark arrays to represent spatial position. The difference is that in hunting waterstriders do not only represent their position with respect to the landmark array, but must also encode the position of the prey in terms of its position relative to the landmarks.

In discussing the various spatial representations of prey position utilized by waterstriders the issue of the importance of vision is a reoccurring one. Waterstriders devote a great deal of their CNS to processing visual input. Behaviourally, the drift compensation mechanism is crucial to stream dwelling waterstriders. Nevertheless, as indicated in chapter three waterstriders do not appear to need visual feedback from the prey to initiate or guide an attack. I have suggested that visual information from the prey item is not a significant factor in waterstrider predation, although their ability to visually identify landmarks for use in spatially representing the prey position is important. The question becomes one of whether or not waterstriders are capable of actually seeing their prey. Results from chapter two suggest that a useful strategy for waterstriders when hunting is to avoid overshooting the target. However, in chapter four, under non-beacon homing conditions waterstriders do, in fact, overshoot the prey's position. Possibly visual feedback from the prey item causes waterstriders to proportionately reduce their stride length to avoid overshooting the prey. This explanation is speculative as I have not systematically investigated waterstriders actually capturing prey. The ants and flies were always removed before the waterstrider could capture them. In the studies presented in chapters two and three this was to prevent the waterstriders from feeding between trials, whereas in chapter four it was because of the desire to study movement patterns under non-homing conditions. In casual observations I have seen that waterstriders will often stride so as to move over and beyond a prey item, attempting to grasp it with their hooked prothoracic legs. On other occasions waterstriders approach more cautiously, move close to the prey, and execute a series of small, quick "hops" in an effort to capture the prey. I suspect that the differences in prey capture technique may be related to the size of the prey. It is one of the many features of waterstrider hunting behaviour that I would like to study further.

Much of the work in the field of insect spatial representation is conducted on members of the social insects, especially the desert ant *Cataglyphis* and the common honeybee. These studies have provided great insight into the abilities and workings of insect memory, navigation, and spatial representation. The studies reported here demonstrate that waterstriders can also serve as an excellent species for investigations of spatial representation. As insects waterstriders are amenable to laboratory testing, are easily housed, and relatively easily maintained. Unlike many other insects, waterstriders are largely confined to a two-dimensional space, that is, the water surface. Ants, for instance, regularly climb vegetation or other objects in their environment, thereby adding a third dimension to the issue of spatiality. In the case of waterstriders, the water surface is as flat an expanse as one can find under natural environmental conditions. Waterstriders also share the wide range of behavioural traits, including a relatively simple nervous system, with other insects that have been used in studying spatial representation. However, unlike the social insects, the workhorses of this field of study to date, waterstriders are not central place foragers. Hence, studying spatial representation with waterstriders can bring a new approach to the discipline, raising and testing different, although related, questions to those investigated with ants and honeybees, for example.

Gallistel (1990) produced an extensive comparative evaluation of spatial representation across species, determining that the navigational abilities of path integration and piloting are widespread throughout the animal kingdom. My studies lead to the conclusion that waterstriders, despite not being central place foragers, share many of the same spatial representation abilities. Such commonalties are interesting because they imply an underlying similarity in requirements for spatial systems in organisms that share very different evolutionary backgrounds and environments.

Future Studies

The work reported in this thesis suggests a number of further questions to be studied with waterstriders. There is additional data yet to be analyzed from the experiment detailed in the chapter four. Although only the strides before and immediately after the prey was removed were analyzed data from numerous strides, sometimes as many as thirty per trial, were recorded on video. In many of these cases waterstriders were observed to engage in what I have described as a search pattern. Analysis of these searches using random walk models or a further elaboration of statistical shape analysis could be applied to the data to investigate issues of how well waterstriders can keep themselves in the vicinity of the former prey over time, how errors accumulate, and whether or not the presence or absence of landmarks influences search patterns. Another study that was planned, but never carried out, involved rotating the landmark array around the testing arena after waterstriders had initiated an attack to further elucidate the importance of landmarks in guiding a waterstrider's movement during predation.

There are a number of additional factors that can be brought into these kinds of investigations. Waterstriders are commonly found in small groups sharing a productive area of a stream or pond. In these situations waterstriders must compete with each other to be the first to reach a prey item. One study I am particularly interested in conducting would involve placing two or more waterstriders in a testing arena before introducing a prey item to see whether or not the presence of additional waterstriders changes attack patterns.

There are also numerous experiments to be run with a single waterstrider and multiple prey items. These studies would be of a more sensory-perceptual nature, investigating type and detail of information waterstriders extract from vibrations produced by prey and what behavioural choices are made as a result. If prey items of different size, and therefore different energy value, are presented simultaneously, can waterstriders determine the more rewarding prey? If positioned at different distances, will waterstriders always go for the larger prey, or take the closer smaller one? There are a number of permutations on these questions that could provide valuable insights into the choice behaviour in predation.

The fact that this research produced useful and interesting information in and of itself is rewarding. However, it has also provoked additional questions about spatial representation, predatory behaviour, the role of sensory modality, and the use of new forms of statistical analysis of movement patterns that will generate future avenues of research.

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Appendix

Test for a common median direction

The following test for a common median direction of two or more distributions, where distributions are assumed to be the same except for median direction is taken from Fisher, Lewis and Embleton (1987) (pp. 30-32, 111-112, and 200).

For the *i*th sample, $i = 1, \ldots, r$, let $(\theta^*_{ij}, \phi^*_{ij})$ be the deviation of (θ_{ij}, ϕ_{ij}) from the pooled sample median $(\hat{\gamma}, \hat{\delta})$, obtained by rotating the sample to the pole $(\hat{\gamma}, \hat{\delta})$ using (1.7) with $A(\hat{\gamma}, \hat{\delta}, 0)$. Similarly, let $(\theta'_{ij}, \phi'_{ij})$ be the deviation of (θ_{ij}, ϕ_{ij}) from $(\hat{\gamma}_i, \hat{\delta}_i)$, the median direction of the *i*th sample (using 3.10) with $A(\hat{\gamma}, \hat{\delta}, 0)$).

Set

$$U_i = \begin{pmatrix} n_i^{-0.5} \sum_{j=1}^{n_i} \cos\phi^*_{ij} \\ n_i^{-0.5} \sum_{j=1}^{n_i} \sin\phi^*_{ij} \end{pmatrix} \qquad i = 1, \ldots r \qquad (1.1)$$

and compute the pooled estimate

$$\Sigma = \sum_{i=1}^{r} (n_i - 1)\Sigma_i / (N - r) \qquad (1.2)$$

where Σ_i is defined for sample number *i* as

$$\Sigma = \frac{1}{2} \begin{pmatrix} \sigma_{11} & \sigma_{12} \\ \sigma_{21} & \sigma_{22} \end{pmatrix} \qquad (1.3)$$

where

$$\begin{aligned} \sigma_{11} &= 1 + \left(\frac{1}{n}\right) \sum_{i=1}^{n} \cos(2\phi'_i) \\ \sigma_{22} &= 1 - \left(\frac{1}{n}\right) \sum_{i=1}^{n} \cos(2\phi'_i) \\ \sigma_{12} = \sigma_{21} &= \left(\frac{1}{n}\right) \sum_{i=1}^{n} \sin(2\phi'_i) \end{aligned} \qquad (1.4)$$

The test statistic is

$$Z^2 = \sum_{i=1}^{r} U'_i \Sigma^{-1} U_i \qquad (1.5)$$

The hypothesis that the distributions have a common median direction is rejected if Z^2 is too large.

To rotate unit vectors and axes, let (θ,ϕ) be the polar coordinates of a unit vector measured relative to a pole in the direction (0,0). For the case in which ψ_0 is set to zero, then the general form of a matrix giving a rotation of the *x,y* and *z* axes with (θ_0,ϕ_0) as the new *z* direction is

$$A(\theta_0,\phi_0,0)=\begin{pmatrix}\cos\theta_0\cos\phi_0 & \cos\theta_0\sin\phi_0 & -\sin\theta_0\\ -\sin\theta_0 & \cos\theta_0 & 0\\ \sin\theta_0\cos\phi_0 & \sin\theta_0\cos\phi_0 & \cos\theta_0\end{pmatrix} \tag{1.6}$$

Then, supposing that the axis (x,y,z) is measured relative to the polar axis (0,0,1) the coordinates (x',y',z') relative to (x_0,y_0,z_0) are required. Determine one end of the (x_0,y_0,z_0) axis in polar coordinates to obtain (θ_0,ϕ_0). Then

$$\begin{pmatrix}x'\\ y'\\ z'\end{pmatrix}=A(\theta_0,\phi_0,0)\begin{pmatrix}x\\ y\\ z\end{pmatrix} \tag{1.7}$$

z' is the cosine of the smaller of the angles between (x,y,z) and (x_0,y_0,z_0).