

Reversal learning and complex maze learning in the spider *Aphonopelma hentzi* (Girard) (Araneae, Theraphosidae)

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Summary

I studied reversal learning of a spatial task (T-maze) and complex maze learning in adult males of the tarantula *Aphonopelma hentzi* (Theraphosidae) in order to evaluate the suitability of this species as a potential subject for studies concerning behavioural plasticity in spiders. The spiders were able to learn a spatial reversal task in a simple T-maze to avoid aversive conditions of bright light and heat. Over 70% of the spiders reached the criterion (70% correct choices/day) for reversal learning after 12 days of training. The amount of time required to reach the goal box decreased significantly as a function of training, from a mean of 138.1 s on day 1 to 60.2 s by day 12. Spiders learned to avoid light and heat in a complex maze (six blind alleys). The criterion for learning (three consecutive trials of <5 errors) was reached by 70% of the spiders after 10 days of training. The mean number of blind alley errors decreased from 104.3 on day 1 to 14.2 on day 14. The amount of time required to travel from the start box to the goal box (running time) also decreased from a mean of 89.4 min to 9.2 min over the same training period. Extinction of the learned response occurred after 4 days of extinction trials. This is the first demonstration of spatial reversal learning and complex maze learning in a spider. The suitability of *A. hentzi* as an experimental subject in learning studies, as well as the adaptive significance of learning in theraphosids, are also discussed.

Introduction

Learning is generally defined as a relatively permanent change in behaviour that results from previous experience (Kimble, 1971; Davey, 1989). As such it represents an experience-dependent modification of enduring internal representations of the external environment (Dudai, 1989; Mangel, 1993). The degree to which an animal is able to modify appetitive behaviours in response to changes in physiological state (motivation) and changing environmental conditions can increase its survivorship (Punzo & Garman, 1989; Mangel, 1993; Stephens, 1993; Punzo, 1996).

The behaviour of arthropods has long been regarded as relatively inflexible and stereotyped (Tinbergen, 1951; Papaj, 1993). Nevertheless, although many of the responses of arthropods fall under the category of closed behavioural programs (Mayr, 1974), there have been numerous studies showing that many arthropods are capable of modifying their behaviour as a result of past experience (see reviews by LeGuelte, 1969; Alloway, 1973; Krasne, 1973; Lahue, 1973; Papaj & Lewis, 1993; Beugnon *et al.*, 1996; Punzo, 1985, 1996; Menzel *et al.*, 1997).

Most studies on arthropod learning have been conducted on insects, with spiders receiving far less attention (Savory, 1934; Lahue, 1973; Popson, 1999; Punzo, 2000a). Some have argued that arachnids exhibit poor

performance in learning studies and do not lend themselves easily to analyses of traditional types of learning such as habituation, sensitisation, classical and instrumental conditioning, and latent learning (Peckham & Peckham, 1887; Thorpe, 1963; Lahue, 1973; Punzo, 1996). Similar statements have been made for some of the lower vertebrates, including amphibians (Brattstrom, 1990). As a result, there has been some reluctance among students of behaviour to investigate learning abilities in certain taxa (Bitterman, 1965, 1975; Punzo, 2000a). However, more recent evidence has shown that this “poor performance” has been overstated (Quinn, 1984; Punzo, 1985, 1996) and is often not a function of diminished capacity, but rather a consequence of researchers asking these spiders to perform tasks that often have no ecological relevance (Punzo, 1980; Gallistel, 1990). For example, animals that are by nature sedentary cannot be expected to perform well in tasks where they are required to move about, unless they are subjected to stimulus conditions (motivational factors) which force them to move and initiate exploratory activities (Bitterman, 1975; Thompson & Boice, 1975; Papaj & Lewis, 1993).

More recent investigations have shown that spiders are capable of modifying their behaviour based on past experience. For example, *Trochosa parthenus* (Chamberlin) (Lycosidae) is able to learn a maze (a type of spatial learning) to avoid a mild electric shock (Punzo, 2000a). *Phidippus audax* (Hentz) (Salticidae) learns the location of prey in a T-maze and also learns to associate a coloured landmark with the presence of prey (Popson, 1999). Wolf spiders learn to associate chemical cues with the presence of prey (Punzo & Kukoyi, 1997) and potential predators (Punzo, 1997). *Phidippus regius* C. L. Koch learns to avoid unpalatable prey as a result of foraging experience (Edwards & Jackson, 1994). *Cupiennius salei* (Keyserling) (Ctenidae) can remember information concerning its previous movements in order to return to a favourable location (Seyfarth *et al.*, 1982). Web-building spiders can learn the position of captured prey within their webs (LeGuelte, 1969; Lahue, 1973; Sébrier & Krafft, 1993).

Spatial learning tasks are known to represent ecologically relevant learning paradigms for vertebrates and invertebrates (Johnston, 1982; Poli, 1988; Punzo, 1985, 1992, 2000a; Benhamou & Poucet, 1996; Beugnon *et al.*, 1996; Biegler & Morris, 1996; Holtzman, 1998). They also provide excellent protocols for researchers focusing on neurochemical mechanisms underlying the learning process (Punzo & Malatesta, 1988; Zola-Morgan *et al.*, 1993; Punzo, 1988, 1991, 1996; White & Salinas, 1998) and the effects of ageing on information processing in invertebrates (Rockstein & Miquel, 1974; Fahrbach *et al.*, 1995) and vertebrates (Huppert & Wilcox, 1997).

The purpose of the present study was to evaluate the suitability of the theraphosid *Aphonopelma hentzi* (Girard, 1854) as a possible subject in learning studies. Very little data exist on the learning abilities of theraphosids (Henton & Crawford, 1966; Punzo, 1988). This is interesting in view of the remarkable longevity

exhibited by many of these spiders (Baerg, 1958; Minch, 1979; Punzo & Henderson, 1999). It has also been argued that the potential for the evolution of more flexible behavioural programs is typically greater in animals that have longer life spans (Ewert, 1980; Poli, 1988). Yet, in spiders, species that are well known for having long life spans have been neglected in studies on learning, despite being easy to maintain and rear in captivity and therefore lending themselves exceptionally well to laboratory studies.

Tarantulas, being notorious for their lethargy, might appear to present serious practical problems for certain learning studies. However, adult males of *A. hentzi* were chosen for this study because they are not as strongly fossorial as females (Baerg, 1958; Punzo & Henderson, 1999), and they are more ambulatory, tending to wander over considerable distances in search of mates (Baerg, 1958; Janowski-Bell & Horner, 1999). They are known to capture prey during these excursions (Baerg, 1958; Punzo & Henderson, 1999). By using males in my experiments, data collection was more feasible. It has been reported that active subjects make better candidates for many types of learning experiments as compared with those which remain motionless for prolonged periods (Thorpe, 1963; Bitterman, 1975; Poli, 1988). In addition, since males of this species can live for several months following their last moult (Baerg, 1958; Punzo & Henderson, 1999) and are known to return to the same shelter site for several consecutive days (unpublished data), there appears to be a real potential for spatial learning abilities to increase survivorship.

In this paper I study the performance of males of *A. hentzi*, a North American tarantula, in various learning tasks including reversal learning of a spatial task (T-maze), and spatial learning (trial and error) in a complex maze (6 blind alleys). In this way, the performance of *A. hentzi* in these tasks can be assessed and compared with other taxa.

Material and methods

Subjects

All spiders used in spatial learning experiments were adult males that had been reared in captivity from egg sacs deposited by captive-bred females collected in Archer County, Texas (1989–1990). Males were used in learning experiments within 72 hr after their last moult. Spiders were housed individually in glass containers and maintained at 21–23°C and 60–65% RH. They were provided with water *ad libitum* and fed on a mixed diet of fruit flies (*Drosophila melanogaster*), mealworms (*Tenebrio molitor*), and small nymphs of unidentified grasshoppers and crickets (*Acheta domesticus*). Prey sizes used were increased as the spiders grew. Voucher specimens have been deposited in the Invertebrate Collection at the University of Tampa.

Reversal learning in a T-maze

A one-choice point T-maze constructed from galvanised iron was used in this experiment. A detailed

diagram and description of this maze can be found in Kimble (1971). To summarise, the walls of the maze were coated with Fluon[™] (a liquid Teflon material) to prevent the spiders from crawling out of the maze. The length of the central alley (runway) was 40 cm, and the arms were 20 cm in length. The alley and arms were 8 cm in width and height. Pilot studies using a different set of males showed that normally sedentary males of *A. hentzi* immediately begin to move about when exposed to bright light and ambient temperatures above 32°C.

A 150-watt photographic lamp placed 40 cm above the centre of the maze as described by Boice (1970) produced the aversive conditions of bright light and heat within the maze. A comparable combination of negative reinforcers have been used successfully as motivational factors in maze learning experiments on other light-averse arthropods and vertebrates that are negatively phototactic or avoid bright light (Alloway, 1973; Brattstrom, 1978; Punzo & Malatesta, 1988). The light used in these experiments resulted in a temperature on the floor of the maze of $34 \pm 2^\circ\text{C}$ (SD). Although aversive, it is at least 6°C below the upper lethal temperature for this species (Punzo, 2000b). Spiders were trained to make a correct response (i.e. choose the correct arm of the maze). One arm of the T-maze (“correct arm”) led to a darkened (enclosed) goal box, lined with strips of Thermex[™] insulation, thereby enabling the spider to escape the aversive conditions on the maze floor. This experiment, therefore, can be interpreted as providing an ecologically relevant reinforcer for *A. hentzi*, since these and other theraphosid spiders will quickly retreat into burrows or rock crevices to escape conditions of bright sunlight and/or high ambient temperatures in the field (Baerg, 1958; Minch, 1977; Main, 1982; Punzo, 1991).

Twenty spiders were subjected to reversal training using a protocol similar to that described by Brattstrom (1978) in his work with lizards. To summarise, each spider was subjected to two tests, each consisting of 20 trials/day over a 12-day training period. In test 1, the spiders were trained to go to the right end of the maze to reach the goal box. In test 2, the same 20 spiders were trained to go to the left (reversal training). Test 2 trials were initiated 24 hr after the last trial to the right. The criterion for learning was 70% correct choices/day (14 out of 20 trials correct/day).

For each trial, a spider was placed at the entrance of the maze. The spider would immediately begin to move along the central alley, arrive at the choice point, and then turn right or left. A response was considered a spatial choice if the spider's rear legs entered either arm of the maze. If a spider made an incorrect choice (moved into the wrong arm), it was allowed to remain in the incorrect arm until it turned around and corrected its error (corrected training procedure). In no case did a spider simply stop at the choice point and remain there, or back up, under these aversive conditions. Once the goal box was reached, the spider was allowed to remain inside for 5 min before the start of the next trial. The floors and walls of the maze were wiped cleaned with a damp soapy sponge followed by a 2% acetone solution

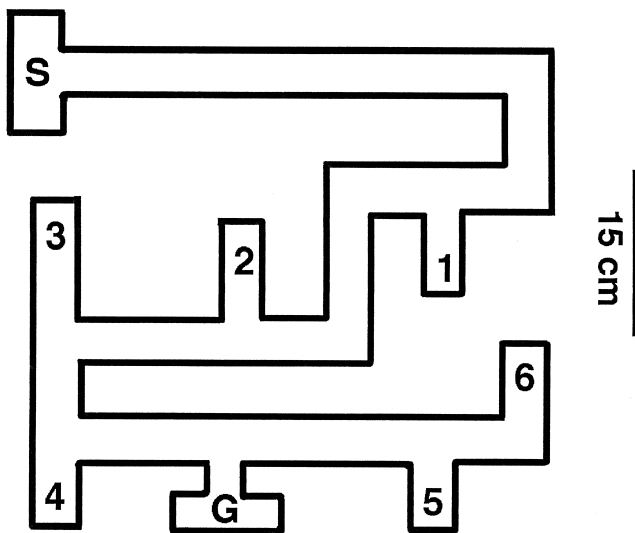


Fig. 1: Diagrammatic representation of the apparatus used for complex maze learning experiments in *Aphonopelma hentzi*. At the beginning of each trial, an individual spider was placed in the start box (S) and allowed to run the maze until entering the goal box (G). The maze consisted of six (1–6) blind alleys. See text for details.

after each trial to remove any odour cues or silk. Previous experiments had shown that these spiders do not react negatively to surfaces where soap or dilute acetone have been previously applied (unpublished data). I recorded the number of errors and correct choices, and the amount of time required to reach the goal box after the beginning of a trial (running time). Results were expressed as the percentage reaching the criterion (Longo, 1964; Northcutt & Heath, 1973; Brattstrom, 1978). All statistical procedures followed those described by Sokal & Rohlf (1995).

Complex maze learning

The maze used in these experiments (Fig. 1) had the same floor plan as that described by Turner (1913) in his study of maze learning in cockroaches and has been subsequently used many times in similar studies with both vertebrates and invertebrates (Kimble, 1971; Alloway, 1973; Bolles, 1975; Punzo, 1980, 2000a). There were six blind alleys (1–6), a start box (S), and an enclosed goal box (G). A sliding wooden panel (fitted across the opening of the start box) was in place before the initiation of learning trials. This prevented the spider from entering the maze. The floor was made of wood and the sides constructed from galvanized iron. Alley walls were sprayed with Fluon[™] as described previously. All alleys had a width of 6 cm.

Aversive conditions (bright light and heat) were used as motivational factors (see above). I used the same procedure as that described by Punzo (2000a) for the wolf spider *Trochosa parthenus*. Twenty different spiders were used in this experiment. Each spider received 10 trials/day over a 14 day training period (acquisition, A). At the start of each trial a spider was placed in the start box (S) for a period of one min. The wooden panel was then lifted, allowing the spider to enter the maze. The

spider was allowed to traverse the maze and could avoid the bright light and heat by entering the enclosed goal box (G) whose top and sides were padded with strips of Thermex[™] insulative material. Trials ended when the spider entered the goal box. The spider was allowed to remain in the goal box for 30 s, then retrieved and placed back in the start box for 30 s before the start of the next trial. After each trial, the floor of the maze was cleaned as described above. I recorded the number of blind alley errors for each trial. By definition, an error occurred when more than half of the spider's body entered a blind alley; this definition is commonly used in maze learning experiments with insects (Thorpe, 1963; Alloway, 1973) and vertebrates (Brattstrom, 1978; Macphail, 1982).

The criterion for concluding that learning had occurred was the number of days required by the spiders to complete three successive trials with fewer than five errors (Lahue, 1973; Brattstrom, 1990). Data were expressed as the percentage of spiders reaching the criterion on each day of testing. Once the criterion had been reached, each spider was subjected to 10 extinction trials/day for six days. Extinction trials (E) were initiated 24 hr after the last day of acquisition trials. During these trials, the goal box was not covered on top. As a result, spiders were still exposed to the aversive conditions even when they entered the goal box.

Results

Reversal learning experiments

The results of the T-maze experiments represent the first demonstration of reversal learning in a theraphosid spider (Fig. 2). A repeated measures ANOVA indicated that these spiders increased their success at correctly completing the maze by reducing their number of errors/day (test 1: $F=7.43$, $p<0.01$; test 2: $F=6.64$, $p<0.01$). In the first T-maze test (test 1; test to the right), 80–85% of the animals reached the criterion by days 11 and 12.

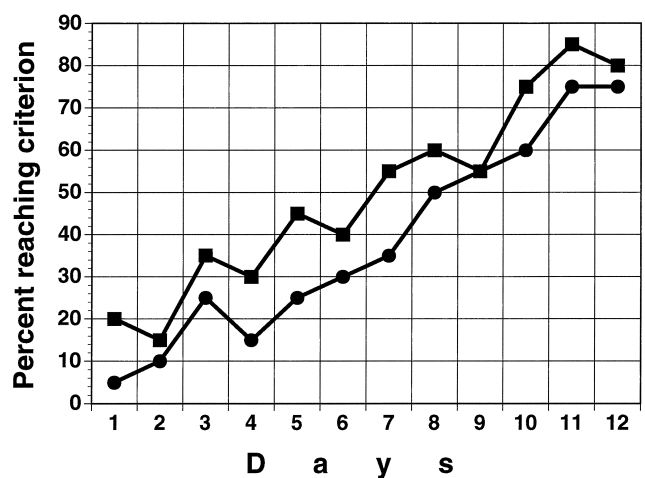


Fig. 2: Results from spatial reversal learning in a T-maze by 20 adult males of *Aphonopelma hentzi*. Values represent the percentage of animals reaching the criterion (70% correct choices/day) over the 12-day testing period. Black squares represent data for spiders from test 1 (turn to the right). Solid circles are for reversal trials (test 2, turn to the left). See text for details.

These results are significantly different from chance ($r=0.887$, $p<0.01$). The reversal learning part of the experiment (test 2; to the left) was more difficult and only 75% reached the criterion by day 12. Under test 1 conditions 55% of the spiders had reached the criterion by day 7 as compared with only 35% under reversal conditions ($G=14.7$, $p<0.01$).

The amount of time required by the spiders to reach the goal box decreased from a mean of $138.1 \text{ s} \pm 8.9 \text{ SE}$ (range 106–158 s) on day 1 to a mean of $60.2 \pm 4.6 \text{ s}$ (range 52–75 s) on day 12. An ANOVA showed a significant effect of learning trials on running time ($F=31.2$, $p<0.001$).

Complex maze learning

The results show that *A. hentzi* was able to learn a relatively complex maze (Fig. 3). A repeated measures ANOVA showed an overall significant effect of days of training on performance ($F=114.7$, $p<0.001$). Over 50% of the spiders had reached the criterion by day 8, and 70% by day 10. There was a significant improvement in performance between day 4 and day 8 of training (Scheffé $F=27.9$, $p<0.01$).

The number of blind alley errors (BAE) decreased from a mean of $104.3 (\pm 21.7 \text{ SD})$ on day 1 of acquisition trials, to 14.2 ± 5.3 on day 14 ($t=23.8$, $p<0.01$). Similarly, the amount of time required to reach the goal box decreased from $89.4 \pm 32.3 \text{ min}$ on day 1 to $9.2 \pm 3.2 \text{ min}$ on day 14 ($t=28.3$, $p<0.01$). Extinction of the learned response was also observed. While 75% of the spiders exhibited the criterion performance on day 2 of extinction, this decreased to only 35% by day 4 (Fig. 3).

Discussion

The results of this study demonstrate the suitability of theraphosid spiders for the comparative study of

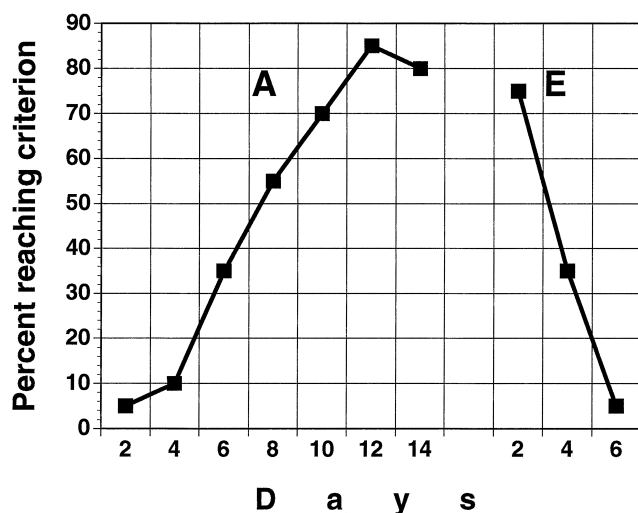


Fig. 3. Results of complex maze learning by *Aphonopelma hentzi* ($n=20$). Data expressed as the percentage of spiders reaching the criterion for learning (three consecutive trials with <5 errors). Data shown for acquisition (A) and extinction (E) trials. Each spider received 10 trials/day. See text for details.

learning in invertebrates. They performed well in a variety of behavioural experiments, require relatively little maintenance compared with many other animals, and numerous species can be easily bred in captivity. In addition, their relatively large body size coupled with a concomitantly large cerebral ganglion (brain), qualifies them as intriguing subjects for neuroanatomical, electrophysiological, and neuroethological approaches to the study of behaviour that employ techniques such as selective ablation and lesioning, and implantation of microelectrodes. My own preliminary studies have shown that adults of *A. hentzi*, *A. echinum* (Chamberlin) and *A. chalcodes* Chamberlin can be readily anaesthetised with CO_2 and exhibit a high rate of recovery ($>80\%$) from surgical procedures which expose the brain (unpubl. data).

The ability of an animal to learn foraging routes or to associate a specific location in two-dimensional space (spatial learning) with the availability of food, shelter sites, or escape routes, can contribute significantly to overall survivorship (Able, 1991; Punzo, 1985; Benhamou & Poucet, 1996; Sahley & Crow, 1998). Indeed, it has been argued that spatial learning ability is a necessary prerequisite for most animals to survive in their natural environments (Staddon, 1983; Holtzman, 1998). *Aphonopelma hentzi* demonstrated the ability to learn spatial tasks (a simple T-maze and a more complex maze). This is the first demonstration of complex maze learning by a theraphosid spider.

In addition, this spider has the ability to exhibit reversal learning, a task studied extensively in vertebrates but virtually unexplored in invertebrates. Animals are often exposed to changing conditions in the availability of required resources such as food, and are well served if they can learn to switch (habit reversal) to food items that might have been avoided when more attractive food items were in greater abundance (Able, 1991; Benhamou & Poucet, 1996; Holtzman, 1998). Similarly, a route that was previously used to return to a reliable source of food may be abandoned in favour of another if food availability changes (spatial reversal) (Longo, 1964; Menzel *et al.*, 1997; Punzo, 2001; Punzo & Bottrell, 2001). It has been suggested that the capacity for reversal learning requires a CNS characterised by a degree of neuroarchitectural complexity greater than that exhibited by most arthropods (Bitterman, 1975; Bolles, 1975; Davey, 1989; Gallistel, 1990). The results of this study, as well as the demonstration of reversal learning in colour- or odour-trained honey bees (Menzel *et al.*, 1997), support a re-interpretation of that view.

There have been few studies on complex maze learning in spiders. The wolf spider *Trochosa parthenus* was trained in the same complex maze used in this study, although it ran the maze to avoid a mild electric shock instead of light and heat (Punzo, 2000a). This spider reached a similar criterion of learning after 7 days of training as compared with more than 10 days for *A. hentzi*. This could be due to the fact that *T. parthenus* is typically less sedentary than *A. hentzi*, and more frequent locomotor activity should enhance maze learning ability. The different types of aversive stimuli employed

in these experiments may have also contributed to the differences in performance between these two spiders. Henton & Crawford (1966) showed that another species of theraphosid, *Aphonopelma californicum* (Ausserer), was able to learn the correct choice response in a T-maze in order to orient toward polarised light, although reversal training capability was not investigated.

The distances that males of *A. hentzi* travel in the search for food, shelter sites, and females are highly variable (Janowski-Bell & Horner, 1999; Punzo & Henderson, 1999). Some tropical theraphosids are arboreal and seek shelter in a specific tree hole from which they emerge at night to hunt for prey before returning to the same refuge (Charpentier, 1992; Stradling, 1994). Many female theraphosids excavate their own burrows or occupy abandoned rodent burrows, where they may remain for long periods of time (Baerg, 1958; Gabel, 1972; Minch, 1977, 1979; Punzo & Henderson, 1999). Abandoned rodent burrows may have several side tunnels and exit holes emanating from the central tunnel. Tarantulas that inhabit such burrows often change their position and/or the location of their egg sacs within these tunnels depending on ambient temperature and relative humidity (Main, 1982; Kotzman, 1990). In all of these cases, the ability to remember specific sites in three-dimensional space could be important for survival and reproduction.

In summary, *A. hentzi* performs well in a variety of learning tasks that have ecological relevance to theraphosids. Its ability to perform well in spatial learning tasks despite its poor visual capacity suggests that it relies primarily on tactile cues and proprioceptive feedback. This spider could serve as a valuable subject for researchers interested in neuroethological, biochemical, anatomical, or behavioural approaches to the comparative study of learning and memory, as well as those interested in parameters that affect the learning process such as stimulus and response contingency patterns, types and schedules of reinforcement, and motivational factors.

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