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Cognitive Abilities of Araneophagic Jumping Spiders

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Introduction

It is widely appreciated that natural selection acting on heritable variation is responsible for the evolution of the morphology and behavior of animals, but the relationship between natural selection and behavioral abilities tends to be more easily overlooked. Learning, for example, is sometimes viewed as generating behavior independent of natural selection but this notion does not hold up to close scrutiny. The term 'learning' has been used for a wide range of mechanisms by which previous experience adaptively alters behavior, and learning of one sort or another appears to be universal in the animal kingdom. Learning depends critically on memory, and the particular things remembered by individuals of a species will vary from circumstance to circumstance. The particular behavior that an animal might learn is not the direct product of natural selection, but an appreciation of natural selection and the species' evolutionary history is critical none the less. The goal in an evolutionary approach to animal learning is to understand how

natural selection has shaped the mechanisms by which the animal processes information from experience and files memory adaptively. We should expect species-specific biases and limitations that reflect the species' evolutionary history.

Baerends' (1939) celebrated study of sand wasps (genus *Ammophila*) illustrates this especially well. When a sand wasp female is ready to oviposit, she digs a chamber in a sand dune, plugs the hole and then flies away. Later she returns with a paralysed caterpillar. Unplugging the concealed chamber, she shoves the caterpillar inside, deposits an egg and then plugs the chamber again. Later, the egg hatches and a hungry larva begins feeding on the paralyzed caterpillar. Each morning, the sand wasp returns to the chamber, unplugs it and assesses the size of the growing larva and shrinking caterpillar. When the female wasp detects that the larva is about to eat up its food supply, she compensates by finding and paralyzing another caterpillar, bringing it to the chamber and replenishing the hungry larva's larder.

Sand wasps are especially remarkable because each female usually tends two or three chambers at the same time, each chamber being in a different location and each larva being at a different stage of feeding and development. Baerends (1939) showed experimentally that the sand wasp learns the configuration of landmarks around each concealed chamber and uses these landmarks to find, and replenish when required, the individual chambers. That is, the wasp learns not only where the chambers are but remembers what action is needed at each.

Most people might have difficulty matching the wasp's skill at nurturing larvae in sand chambers but, nevertheless, far surpass the wasp at many other learning tasks. The wasp's learning ability is specialized in a way that is understandable when we appreciate its species-specific evolutionary history. In the world in which the sand wasp evolved, the ability to monitor sand chambers has been critically important.

The sand wasp also provides an especially instructive example of why nature–nurture is a sterile distinction. Learning is not an alternative to natural selection but, instead, in its species-specific details, an evolved adaptive ability (Lorenz, 1969; Johnston, 1982; Miller, 1988; Gottlieb, 1997). Extrapolating from the sand wasp example, we should generally expect an interrelationship between learning and instinct (Fig. 14.1), with a prevalence of species-specific biases, limitations and idiosyncratic features that reflect the species' evolutionary history predominating.

Learning overlaps with a more controversial topic – animal cognition. In lay terms, cognition is reasoning, thinking and mental problem-solving. With Western philosophy's heritage from Descartes (1637), it has long been viewed as somehow disreputable even to discuss the topic of animal cognition, partly for fear that the next step would be acceptance of the notion of animal minds. For Descartes (1637), all animals are automatons, but this is a difficult position to maintain in the face of modern animal studies. For example, we

INSTINCT/INNATE   LEARNING
(<FLEXIBLE)   (>FLEXIBLE)

┃   --- CONTINUUM ---   ┃

PREDICTABLE   UNPREDICTABLE
FEATURE   FEATURE
IN GENETIC FUTURE   IN GENETIC FUTURE

GENETIC BASIS

VIRTUALLY ALL ANIMALS,
INCLUDING HUMANS,
HAVE AN
INSTINCT TO LEARN.
AND EVEN THE MOST
"RIGID"OR "FIXED"
INSTINCTIVE BEHAVIOR
MAY INVOLVE REFINEMENT
THROUGH EXPERIENCE.

Fig. 14.1   Diagram showing relationships among the genome, instinctive behavior and learned behavior.

can refuse to call the problem-solving skills of African Grey Parrots (Pepperberg, 1990, 1992, 1994) avian cognition only at the risk of drastically denying the common-sense meaning of the term. However, global, all-purpose ability is not what we should expect when we study animal cognition any more than with animal learning. Instead, we should expect, with both learning and cognition, focused ability with idiosyncratic biases and limitations reflecting the species' evolutionary history.

Regardless of how useful it might be for an animal to have pronounced learning and cognitive abilities, we would expect size (more specifically brain size) to impose a ceiling on what can evolve (Gottlieb, 1997). Conceding that large-brained animals such as birds and mammals may have interesting cognitive ability is one thing, but what about spiders? The notion of a cognitive spider might seem almost ludicrous: even if some of the birds and mammals are not automatons, surely all of the spiders, insects and other arthropods are? After all, arthropods are only distantly related to *Homo sapiens* and, besides, a spider's brain is minute compared to that of birds and man. In fact, it is tempting to argue that the restriction to easily tractable (noncognitive) behavior in arthropods is a good reason to use these 'simple' animals in behavior research. The attitude of the present authors was close

to this when, many years ago, we first became interested in arthropod behavior. Evidently we were wrong, and in this chapter we review recent work on *Portia*, the spiders that changed our minds.

Spiders that eat other spiders

Portia, a genus of araneophagic (i.e. spider-eating) jumping spiders (family Salticidae), appears to have the most versatile and flexible predatory strategy known for an arthropod (Jackson, 1992a, 1996). How animals incorporate deceit into their communication strategies has long been a topic of special interest in discussions of animal cognition (Mitchell, 1986), and a dominant feature of *Portia*'s predatory strategy is aggressive mimicry, a system in which the predator communicates deceitfully with its prey (Wickler, 1968; Endler, 1981).

Typical salticids do not build webs. Instead, they are hunters that catch their prey in stalk-and-leap sequences guided by vision (Forster, 1982). Salticids differ from all other spiders by having large anteromedial eyes and acute vision (Land, 1969a,b, 1985). However, the behavior of *Portia* is anything but typical for a salticid. There are some 15–20 species in this genus of African, Asian and Australian spiders (Wanless, 1984), but most of what we know comes from studies of five species, *P. africana*, *P. albimana*, *P. fimbriata*, *P. labiata* and *P. schultzi* (Jackson, 1992b).

Besides hunting prey cursorially, *Portia* also builds a prey-catching web (Jackson, 1986). The typical prey of the salticid is insects, but *Portia*'s preferred prey is other spiders (Li and Jackson, 1996, 1997). *Portia* frequently hunts web-building spiders from other families by invading their webs and deceiving them with aggressive-mimicry signals (Fig. 14.2). While in the other spider's web, *Portia* will also raid its victim's eggsacs, take insects ensnared in the web, or even take food directly from the mouth of the other spider (Jackson and Blest, 1982a; Jackson and Hallas, 1986a).

In the simplest instances, *Portia* makes aggressive-mimicry signals by moving legs, palps, abdomen or some combination of these to make web-borne vibrations. *Portia*'s typical victim, a web-building spider but not a salticid, typically lacks acute vision (Land, 1985) and instead perceives the world it lives in largely by interpreting tension and vibration patterns in its web (Witt, 1975). With its signals, *Portia* can gain dynamic fine control over its prey's behavior.

Different kinds of web-building spiders are most readily deceived by different web signals. As long as the web-building spider is in a suitable size range (about one-tenth to two times *Portia*'s size), *Portia* is effective at deceiving and preying on it. This is true not only for a diverse array of web-building spiders in each *Portia* species' natural habitat, but also for
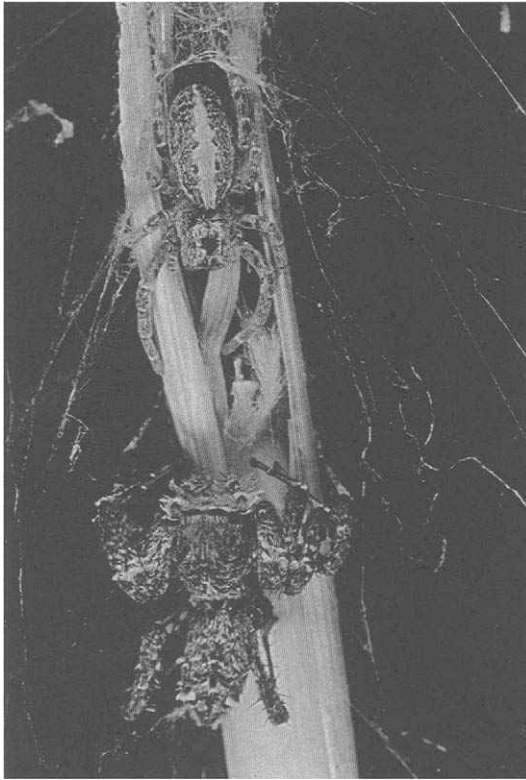
Fig. 14.2 *Portia labiata*, the lower spider, deceitfully lures a member of the social spider *Stegodyphus sarasinorum* up close by signalling on the *S. sarasinorum*'s web with light palp plucks. Shortly after this photograph was taken, *Portia* lunged forward and captured the duped spider. Photograph by R. S. Wilcox.

species given to *Portia* in the laboratory that would never be encountered in nature.

Early in our research, understanding how *Portia* derives the appropriate signals for different types of prey became a primary objective. The emerging conclusion from this work, which is still in progress, is that *Portia* uses an interplay of two basic tactics (Jackson and Wilcox, 1990, 1993a,b): (1) it uses specific preprogrammed signals when cues from some of its more common prey species are detected; and (2) it also adjusts signals in a flexible fashion, as a consequence of feedback from the victims.

Next, we shall review a particularly striking example of *Portia*'s use of preprogrammed signals, and with this example also illustrate the potential for prey defense and predator–prey coevolution.

## Predator–prey interactions between *Portia fimbriata* and *Euryattus* sp.

In the rain forest of Queensland, Australia, the prey of *Portia fimbriata* includes an undescribed species from the salticid genus *Euryattus*. *Euryattus* sp. is not a typical salticid and *P. fimbriata* uses a unique tactic against this one species of prey. For shelter and oviposition sites, most salticids spin small silk cocoons (Jackson, 1986), but *Euryattus* females take shelter and lay their eggs inside curled-up leaves suspended by silk strands from tree trunks, rocks or vegetation. The male of *Euryattus* courts the female by cautiously venturing onto the leaf and, by making vibratory signals on the leaf surface, luring the female out into the open (Jackson, 1985). However, *Euryattus* females also receive unwelcome visitors.

Adult females of *Euryattus* and *P. fimbriata* are comparable in size. The adult females and large juveniles, but not the smaller juveniles or the males, of *P. fimbriata* take a special interest in suspended leaves (Jackson *et al.*, 1998): even if reared in the laboratory with no prior contact with *Euryattus*, they move out on to the leaf and make signals closely resembling the calling signal of the *Euryattus* male (Wilcox and Jackson, unpublished data) (Fig. 14.3). Lured out by this counterfeit signal, the *Euryattus* female is captured by the hungry *Portia* (Jackson and Wilcox, 1990).

Interactions between *P. fimbriata* and *Euryattus* are of interest not only because they illustrate extreme focusing of preprogrammed tactics (species-specific signal imitation). These interactions also provide evidence of predator–prey coevolution. Owing to its markings, tufts of hairs and long, spindly legs, *Portia* does not have the appearance of a typical spider, resembling instead a piece of detritus. Also, *Portia*'s stepping gait is normally slow and choppy, rendering *Portia* difficult to recognize even when moving. In Queensland, *P. fimbriata* feeds on a variety of salticids in addition to *Euryattus* sp., catching these other species out in the open by stalking up behind them. If the salticid being stalked detects movement and turns to look at *Portia*, it normally peers at what appears to be no more than a piece of detritus and then turns and continues on its way, and to its doom (Jackson and Blest, 1982a).

Euryattus sp. is, among salticids, an exception. When seen, an approaching *P. fimbriata* is recognized by *Euryattus* sp. as a predator and driven away. To drive *P. fimbriata* away, *Euryattus* sp. comes out of the rolled-up leaf, then suddenly and violently leaps at or charges toward the *P. fimbriata*, sometimes banging head-on into and knocking away the unwelcome guest. Once attacked, *Portia* flees and *Euryattus* survives (Jackson and Wilcox, 1990).

The facility of *Euryattus* sp. at recognizing *Portia* is apparently pre-programmed: individuals reared from eggs in the laboratory and never exposed to a *Portia* beforehand still behave in this manner the first time they encounter the predator (Jackson and Wilcox, 1990). Also, this predisposition
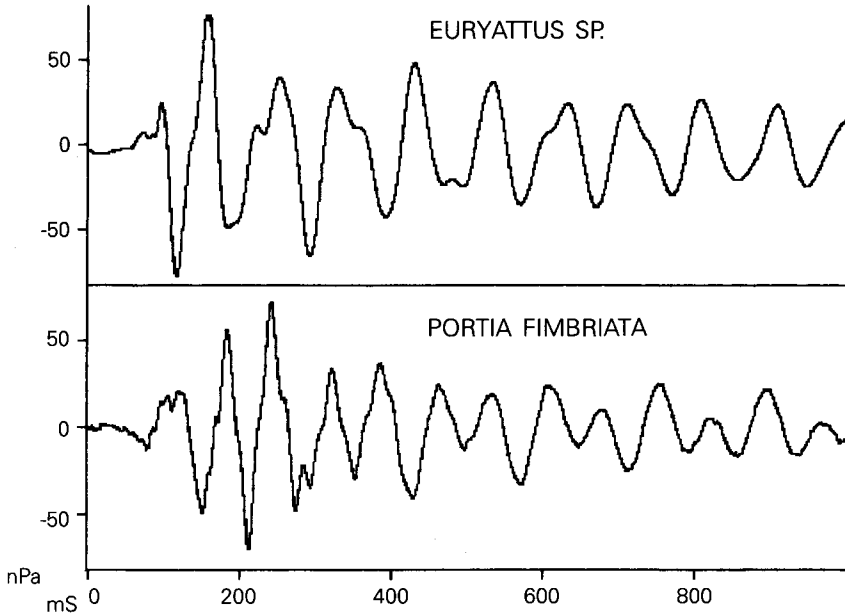
Fig. 14.3 Top: the mating signal of a male of the jumping spider *Euryattus* sp., from the rain forest in Queensland, Australia. Males make this signal while on top of a hanging, curled-up leaf. Females of *Euryattus* reside within the curl of the leaf, which they hang in the air with supporting anchor threads. This signal appears to induce the female out of the leaf, to mate with the male. Bottom: the signal made by adult female of *Portia fimbriata*, recorded from the same leaf as in the above. *P. fimbriata* lures the female to the entrance of the curl with the signal, then attacks the female and eats her. (Wilcox and Jackson, unpublished data.)

to recognize *P. fimbriata* appears to be unique to a population where *Euryattus* sp. and *P. fimbriata* are sympatric. *P. fimbriata* is absent from another population sampled about 15 km away from the habitat where *Euryattus* and *P. fimbriata* are sympatric. In tests using laboratory-reared spiders, allopatric *Euryattus* only rarely defended themselves against stalking *P. fimbriata*, and *P. fimbriata* was more effective at capturing allopatric than sympatric *Euryattus* (Jackson and Wilcox, 1993a).

These studies suggest that, in Queensland, *P. fimbriata* and *Euryattus* have been involved in a coevolutionary 'arms race' (Dawkins and Krebs, 1979), in which improvement in the predator's ability to capture the prey selected for improvement in the prey's ability to defend itself and vice versa. The potential for such arms races may partially account for the evolution of exceptional complexity in the araneophagic spider's predatory strategy (Jackson, 1992a). Next, we shall review some other examples of prey that have *Portia*-specific defenses.

Detecting *Portia*'s footsteps

The tightly strung, intertwining silk threads that make a spider's web appear to be an extraordinarily sensitive component of the web-building spider's tactile sensory system (Masters *et al.*, 1986). When going into the other spider's web, remaining silent (i.e. making no tactile or tension cues that would be detectable by the resident spider) is probably next to impossible for *Portia*. The alternative, and the strategy *Portia* adopts, is almost the antithesis of remaining silent: *Portia* deliberately broadcasts deceitful signals.

Often there is a need for *Portia* to walk into the web, and this may present a problem because a repetitive walking gait might alert the resident spider to the presence of an intruder. *Portia* seems to compensate for this problem. Unlike that of a typical salticid, *Portia*'s walking gait is slow and choppy. Each leg tends to move out of phase with each other leg, and the speed, amplitude and phasing of each leg's movements in relation to other legs change continuously (Jackson and Blest, 1982a). Most spiders do not respond to this nonrepetitive gait, the more or less patternless signals probably registering as mere noise.

Yet, as striking exceptions, a select few of species of web-building spiders tend to react with a special kind of panic, which we call '*Portia* panic'. We have tested these species in the field and the laboratory by having, besides *Portia*, numerous other types of spiders walk across their webs. When the intruder was a spider other than *Portia*, these species normally did no more than run to the edge of the web, but when *Portia* walked on their webs, they leapt out and continued running until they were far away. For these species, there is no panic like *Portia* panic! Experimental studies in progress indicate that it is *Portia*'s slow, choppy gait that panics these special prey of *Portia*, and that prior experience with *Portia* is not necessary. For these species, the cues for panic appear to be the more or less patternless signals from *Portia*'s nonrepetitive gait (Jackson and Wilcox, unpublished data), the very features of the gait that seem to conceal *Portia* from most prey (Table 14.1).

Portia panic appears to provide additional examples, along with *Portia–Euryattus* interactions, of predator–prey coevolution. *Portia* panic also illustrates how signalling and disguise interrelate. Next, we shall examine another type of disguise in *Portia*'s repertoire, what we call 'smokescreen tactics'. Smokescreen tactics are used against a wide range of web-building spiders, but they are especially important when *Portia* attempts to catch '*Portia*-panicked' spiders.

Smokescreen tactics

We first became aware of smokescreen behavior when trying to record *Portia*'s signals in the field using a transducer connected by a stylus to the

Table 14.1 Results of introducing *Portia** and non-*Portia*[†] intruders on to webs of prey spider species known to be panicky species. Intruders were introduced on to the web of the prey spider and the response of the prey spider scored as to whether it left its web entirely (panicked) or stayed on its web, even if it only maintained contact with the web with one leg. The results show the percentage times the prey species panicked and, in parentheses, the total number of trials per prey species. The results clearly show a significantly greater number of panic responses to *Portia* than to non-*Portia* intruders χ^2-test of independence, $p < 0.001$). (Wilcox and Jackson, unpublished data.)

Panicky species	*Portia* intruders	Non-*Portia* intruders
Hygropoda dolomedes	63 (120)	0 (151)
Hygropoda sp.	50 (36)	0 (38)
Dendrolycosa sp. A	59 (81)	0 (23)
Dendrolycosa sp. B	61 (98)	0 (43)
Underleaf pholcid	58 (79)	0 (148)
Psilochorus sp.	44 (59)	0 (123)
Average %/total *n*	56 (473)	0 (526)

*Portia intruders used: *P. africana*; *P. fimbriata*; *P. labiata*; *P. schultzi*. All are aggressive mimics.
[†]Non-*Portia* intruders used: (family Salticidae) – *Bavia aericeps*; *Cyrba ocellata*@; *Euryattus* sp.; *Jacksonoides queenslandica*; *Mopsus mormon*; *Plexippus pyakulli*; *Simaetha paetula*; *Tauala lepidus*; *Trite planiceps*; (Gnaphosidae) – *Lampona cylindrata*@; *Taieria erebus*@; (Mimetidae) – *Mimetus maculosus*@; (Pholcidae) – *Pholcus phalangoides*@.
Species denoted @ are aggressive mimics.

web. This work was frustrating on windy days because air movement caused large-scale displacement of the web which tended to mask out the signals we were trying to record from *Portia*. Eventually we realized that not only did the wind mask *Portia*'s signal but also it was when the wind blew that *Portia* was especially likely to walk across the web toward the resident spider. Later, in laboratory experiments, we demonstrated that *Portia* opportunistically times its advance across the web when there is background noise from wind or from the struggles of insects on the web (Wilcox *et al.*, 1996).

Portia is remarkably discriminating in its use of the opportunistic smokescreen tactic, reserving this tactic for when stalking a spider in a web, and not using it when stalking the web-building spider's own prey (an ensnared insect) or its eggsacs (Wilcox *et al.*, 1996), both of these being food items against which the smokescreen would be meaningless.

More recently, we have discovered that, when the wind is not blowing, *Portia* may make its own smokescreen. The self-generated smokescreen is a long train of low-frequency vibrations of the silk made by *Portia* flexing suddenly and violently, then more slowly relaxing its legs so that its body rocks up and down in the web. *Portia* proceeds to make its advance toward

Table 14.2 Analysis of signals made by ten individual *Portia fimbriata* (Q) when *P. fimbriata* was stalking *Badumna longinquus*. Data show the percentage of forward movement made by *Portia* during smokescreen signals and during an interval of 1.0 seconds after non-smokescreen signals were made. *Portia fimbriata* always moved forward during smokescreen scored for this study. In addition to the data below, we recorded 388 episodes during which *Portia* made non-smokescreen signals but no forward movement was made. Predator/prey body size = 1.0. Results show a significantly greater forward distance made during signal production than during no signal production (χ^2-test of independence, $p < 0.001$). (Wilcox and Jackson, unpublished data.)

Episodes during which *Portia* moved forward	Number of episodes	Percentage of total forward movement
Smokescreen signals	293	86.4
Non-smokescreen signals	36	10.6
Smokescreen plus non-smokescreen signals	329	97.1
No signal made	10	2.9
Total	339	100.0

the resident spider primarily while the web is reverberating with this signal (Table 14.2), and this self-generated signal appears to mask the more subtle web vibrations made by *Portia*'s footsteps.

By using smokescreens (either opportunistic or self-generated), *Portia* combines elements of stealth with aggressive mimicry, behaves with remarkable flexibility and manages to catch even '*Portia*-panicked' prey. However, another tactic of *Portia*'s, trial and error, may be an even more pronounced spider example of flexible behavior.

Flexibly adjusting signals to prey behavior

We originally viewed the trial-and-error tactic as a default tactic used by *Portia* in encounters with those prey for which it lacked preprogrammed behavior. In the field, what appeared to happen in many instances was that *Portia* entered a spider's web and began broadcasting a wide array ('kaleidoscope') of different signals. The kaleidoscope continued until the prey spider responded appropriately, after which *Portia* continued to produce the signal which worked (Jackson and Wilcox, 1993b). If, with the passage of time, the prey spider ceased to respond appropriately to the signal, *Portia* reverted back to the kaleidoscope until a new and effective signal was found.

In laboratory experiments, we confirmed that *Portia* uses feedback from prey behavior to adjust signalling flexibly (Jackson and Wilcox, 1993b). In these experiments, we controlled the way in which the prey spider responded

to the signalling *Portia*. For example, by using an electromagnetic field from a wire coil to drive a magnet glued to the prey spider's dorsum, we could pair up appropriate prey movement with randomly chosen signals from *Portia*'s kaleidoscope. In these experiments, *Portia* consistently narrowed its signal production to the signals we chose at random to reward (Jackson and Wilcox, 1993b).

For how long *Portia* will remember a signal derived by trial and error is not known, but the tactic requires at least short-term memory for the period of the predatory sequence. The longer the memory period, then perhaps the more interesting the trial-and-error tactic becomes as an example of operant conditioning and learning. However, what may be of greater interest is that this tactic enables *Portia* flexibly to derive appropriate signals for just about any type of spider, even species with which it would never have had contact with any time in its evolutionary history.

Even when *Portia* has a preprogrammed tactic for a spider species, trial and error still has a role. Often *Portia* appears to use preprogrammed signals not so much to provide a solution, all by itself, for the problem of how to capture a particular spider but, instead, to get the predatory sequence off to a good start, after which *Portia* finishes the job by trial and error. The victim spider may, for instance, start approaching slowly, then lose interest, become distracted, or begin approaching too fast. When, for any reason, preprogrammed signals do not work, *Portia* switches to trial and error (Jackson and Wilcox, unpublished data).

With the trial-and-error tactic, *Portia* shows an ability to discern what happens after making different signals and to adjust subsequent signalling accordingly. Can this spider also discern and adjust to the predicted consequences of different actions without actually acting first? Doing the calculations in its head, so to speak, would be closer to the common-sense meaning of cognition or thinking.

Making detours and planning ahead

Ability to take indirect routes to a goal (detouring) has been illustrated and studied extensively in vertebrates (von Frisch, 1962; Curio, 1976; Collett, 1982; Chapuis, 1987; Rashotte, 1987; Regolin *et al.*, 1994, 1995a,b). Examples of spiders taking deliberate detours are less well known. Although there were some earlier reports that salticids make detours while in pursuit of prey (Heil, 1936; Curio, 1976), the first detailed experimental confirmation was Hill's (1979) work using North American species of *Phidippus*. The detours required in these experiments were simple and short, and Hill (1979) concluded that detouring required no great insight on the salticid's part because, in the absence of a straight path to the prey, all the salticid did was to head towards an object ('secondary goal') that would bring it closer to

the prey (the 'primary goal') and continue doing this until the prey was reached.

Portia, however, takes long, complicated detours in the field (Jackson and Wilcox, 1993c), including detours in which *Portia* first moves away from the prey before heading towards it. Although detours are a feature of *Portia*'s pursuit of a wide array of prey spider species, the most vivid illustration is in interactions between *P. fimbriata* and *Argiope appensa* in Queensland (Jackson, 1992c).

A. appensa builds an orb web close up against a tree trunk. Simply to walk straight from the tree into the web may appear easy for *Portia*, but there is a problem. *A. appensa* is acutely sensitive to anything foreign in the web. When an intruder is detected, whether *Portia* or some other araneophagic predator, *A. appensa* pumps on the web by rapidly flexing its legs over and over again, setting the web into motion, and either driving or throwing the intruder out of the web (Jackson *et al.*, 1993).

Yet, *P. fimbriata* usually succeeds at capturing *A. appensa*. During typical sequences in the field, *Portia* walks up the tree trunk toward *A. appensa*, stops, looks around, then goes off in a different direction, only later to come out above the web. There are usually vines and other vegetation near the tree and often some of the vegetation extends out above the web. After looking at the web and the surrounding environment (Jackson, 1992c; Jackson and Wilcox, 1993), *Portia* moves away, often going to where the web is completely out of view, crosses the vegetation and comes out above the web. From above the web, *Portia* drops on its own silk line alongside, but without touching, the web of the *A. appensa*. Then, when parallel with the spider in the web, *Portia* swings in to make a kill.

Not only does *Portia* solve the problem of how to capture this hypersensitive prey spider without touching the web, but it also appears that *Portia* takes deliberate detours to reach an optimal approach. Some of these detours observed in nature were over 1m in length and took over 1 hour to execute (Jackson and Wilcox, 1993).

Laboratory experiments have confirmed that indirect routes taken by *Portia* against a wide range of prey are deliberate detours requiring movement to where the prey can no longer be seen and movement sometimes initially away from the prey before reaching it (Tarsitano and Jackson, 1992, 1994). In more recent experiments, *Portia* had to choose between two long and twisting paths, only one of which led indirectly to a prey spider. At the start of the test, *Portia* was on a platform high enough so that the prey was in view, but the prey went out of view once *Portia* descended the platform. In these tests, *Portia* took the route that led to the prey ('correct route') significantly more often than the route that did not lead to the prey ('incorrect route'). In some of these tests, this was despite *Portia* having to walk past the beginning of an incorrect route in order to reach the beginning of the correct route (Tarsitano and Jackson, 1997).

It is difficult to escape the conclusion that *Portia* solves detour problems in its head, makes plans and then acts on these plans. What precisely is meant by the term 'cognition' may not always be clear, but it would be contrived to deny at least the rudiments of cognition in *Portia*.

Cognitive levels

With the topic of animal cognition, as with related topics such as intelligence, awareness, minds and consciousness (Dennett, 1991), attempts to apply precise, logical definitions to examples from real animals quickly become futile Aristotelian exercises (Dennett, 1995). Generally, it is more useful to sidestep the problem of definition and focus on attributes related to cognition, discussing these in relation to interdependent stages or levels (Eysenck and Keane, 1990). From this perspective, cognitive ethology has relevance extending beyond the vertebrates.

In a framework applied initially to the behavior of Honey Bees (Dukas and Real, 1993), cognition was addressed in relation to reception, attention, representation, memory, problem-solving, communication and language. This framework differs from tradition by reducing the emphasis placed on learning and memory. It may be instructive to examine *Portia*'s predatory behavior in relation to this framework.

Reception

Considerations of an animal's sensory reception and processing systems is perhaps the most elementary level at which cognition is relevant. Generally, spiders rely heavily on chemical and tactile cues (Foelix, 1982), but most spiders have poor eyesight (Blest, 1985). Salticids are the primary exception, this family of spiders having unique complex eyes and visual acuity exceeding that known for any other animals of comparable size (Land and Fernald, 1992). Understandably, the tradition in literature on salticids has been to emphasize vision as the modality mediating interaction with prey, predators and conspecifics (Richman and Jackson, 1992). Yet, *Portia* and other salticids also make extensive use of sensory systems based on chemical cues (Pollard *et al.*, 1987; Willey and Jackson, 1993; Clark and Jackson, 1994a,b, 1995a,b) and silk-mediated tactile cues (Jackson, 1982, 1986). Salticids appear not to have substituted vision for other sensory modalities; instead, they appear simply to have added on vision with no particular detriment to their facility at using other modalities (Jackson and Pollard, 1997).

Unlike the more familiar plan of vertebrate and insect eyes, salticid principal eyes are put together very differently (Homann, 1928; Land, 1974). *Portia* has four pairs of eyes, but it is the pair of very large anterior median

eyes (known as the 'principal eyes') that is responsible for acute vision (Land, 1969a,b). Three pairs of smaller secondary eyes, situated either side of the principal eyes, serve as highly proficient motion detectors (Land, 1971, 1974).

The retinae of the principal eyes have a four-layered tier arrangement (Land, 1969a). Light entering through the corneal lens passes successively through layers 4, 3 and 2 before reaching layer 1. In the central area of layer 1 (the fovea), receptors are packed especially close together (about 1 μm apart). The fovea, being the only region that receives a sharply focused image, must be primarily responsible for shape recognition (Blest *et al.*, 1990).

The eye of an average mammal is much larger than the salticid principal eye, and it would be tempting to argue on a priori grounds that the small salticid eye has to be severely limited. Yet, *Portia*'s eye has acuity rivalling that of a primate (Land, 1974, 1985; Blest *et al.*, 1990). Perhaps there is a parallel lesson regarding cognition. On a priori grounds, it is tempting to conclude that a spider's central nervous system, being so small compared to that of birds and mammals, could not possibly support more than the most rudimentary cognitive ability. Yet, as with visual acuity, there appear to be mechanisms, although poorly understood, that go a long way toward overcoming whatever limitations are imposed by small size.

We are only beginning to understand the visual discrimination abilities of *Portia*, but it is clear that a variety of different types of spiders and webs can be recognized from distances of up to about 30 body lengths away on the basis of optical cues alone (Jackson and Blest, 1982b; Clark and Uetz, 1990; Jackson and Tarsitano, 1993; Jackson, 1995; Li and Jackson, 1996, 1997) despite the fact that there are at most a few hundred receptors in the principal eye fovea (Land, 1985). The principal eye is an active eye, and this may be the key to understanding shape perception (Land, 1969b). Scanning (rapid side-to-side and rotary movement of the eye tubes) may enable the salticid to use its small retina to search for recognition cues.

The evolution of acute vision may have been critical in setting the stage for exceptional cognitive ability (Jackson, 1992a). Being able to see, locate and identify quiescent prey before entering a web, *Portia* has available distance and time in which to implement complex tactics. When interacting with an active prey, acute vision means that *Portia* can accurately track, from a distance, the prey's changing location, speed, orientation and behavior. It is difficult to envisage other sensory systems known for spiders operating in a comparable way.

Invasion of webs and use of aggressive mimicry are known for poor-sighted spiders from various families other than the Salticidae. In contrast to *Portia*, these areaneophagic species tend to specialize on a comparatively narrow range of prey spiders, and appear to have considerably simpler and less flexible predatory behavior (Jackson and Whitehouse, 1986; Jarman and Jackson, 1986; Whitehouse, 1986; Jackson and Brassington, 1987).

Attention

Cognitive attention is a many-faceted topic encompassing focused informa-
tion processing in the face of multisensory input (from both internal and
external sources), selective attention, attentional limitations in foraging and
search imagery (Dukas and Real, 1993). Questions related to attention have
not been explicit objectives in our research, but research in this realm is likely
to be rewarding. For instance, while making a detour in pursuit of a prey
item, *Portia* frequently moves along a path on which it can no longer see
the prey and persists on this path for minutes or even hours at a time (Jackson
and Wilcox, 1993a). Also, signalling sessions on webs can last for hours or
even days at a time (Jackson and Hallas, 1986a,b), and more recent studies
by Robert Clark (unpublished) indicate that *Portia* makes use of search
imagery.

Representation

Representation, discussed in relation to cognitive (or mental) mapping, has
received a great deal of attention (Gallistel, 1989). In a broad sense, a
cognitive map is an internal representation of geometric relations among
noticeable points in an animal's environment. In a more narrow sense, a
cognitive map is computational ability, involving learning, problem-solving
and memory. Demonstration of cognitive mapping requires unequivocal
evidence showing that the animal computes a route between two points
without having travelled along this route before (Wehner and Menzel, 1990).
Portia's detouring behavior appears to provide this kind of evidence. After
recognizing prey for which an indirect approach is appropriate, *Portia*
apparently plans a solution to the problem of how to reach the prey along
a path over terrain never crossed before (Tarsitano and Jackson, 1997).

Communication and language

Perhaps this is where *Portia* is left behind. Verbal communication, being
abstract and based on more or less arbitrary symbols, is an ability developed
to a much greater degree in humans than known for any other animals
(Dennett, 1996). Indeed, verbal communication was at one time widely
regarded as uniquely human, but it has become difficult to deny that the great
apes (Premack, 1986) and African Grey Parrot (see Pepperberg, 1990) have
at least a rudimentary capacity for symbolic communication.

   Communication is central to *Portia*'s aggressive-mimicry strategy, but
Portia's signals appear to function more as sensory exploitation (Proctor,
1992; Clark and Uetz, 1993; Ryan and Rand, 1993) rather than a verbal
language. By walking into another spider's web, *Portia* enters the other

spider's perceptual world, since the web is an extension and critical component of the web-building spider's sensory system. Once in the web, *Portia* indirectly manipulates the prey-spider's behavior by exploiting biases in how the prey spider processes web signals.

The most straightforward instances of sensory exploitation are sequences during which *Portia* makes preprogrammed or derived (by trial and error) signals to which the resident spider responds the same as it would respond to a small insect ensnared in the web. If the resident spider is relatively small and harmless, then *Portia* can capture the victim when it comes close, but the tables are likely to be turned when the resident is large and dangerous (Jackson, 1992a). Yet, *Portia* deceives and captures an enormous range of spider species, including the large and dangerous (Jackson and Hallas, 1986b). We are only beginning to understand the variety and subtlety of what *Portia* achieves during signalling bouts. For example, if the resident spider is a large and dangerous spider, *Portia* might lure it in very slowly or, instead of luring the resident spider in, stalk across the web and attack while keeping the resident spider calm but out in the open with monotonous repetition of habituating signals (Jackson and Wilcox, unpublished data).

Verbal communication in *Homo sapiens* and some other vertebrates, being based on more or less arbitrarily assigned symbols, is extraordinarily flexible. *Portia*'s signals, functioning as sensory exploitation, appear quite the opposite of arbitrary, but this does not imply inflexibility. With every appendage plus the abdomen able to move independently at different and changing rates and amplitudes, and in different and changing phase relations to each other, *Portia* appears capable of making virtually an unlimited array of different web signals (Jackson and Blest, 1982a; Jackson and Hallas, 1986a).

How *Portia*'s prey, web-building spiders, responds to signals varies considerably between species and also with the sex, age, previous experience and feeding state of the spider. Yet, *Portia* deceives and preys on just about every kind of web-building spider imaginable, as long as it is about one-tenth to twice *Portia*'s size (Jackson and Hallas, 1986a). Although we have only begun to understand how *Portia* chooses, from its large repertoire of signals, the particular signals that are appropriate for particular spiders, it is clear that this is a communication system based on a high level of flexibility.

Levels of deception

In a review of how animals use deception, Mitchell (1986) specified a classification scheme (Table 14.3) which provides an interesting perspective from which to consider *Portia*. *Portia* is a straightforward example of the first two 'levels'. Level I (deception by appearance) is illustrated by *Portia*'s camouflage (detritus mimicry). For level II, the best-known examples might be angler fish (Gudger, 1946) and firefly *femmes fatales* (Lloyd, 1986), but

Table 14.3 A summary of the levels of deception, with examples. (From Mitchell, 1986.)

Level	Deception is effected by appearance	Program	Examples of deceiver	Examples of deceived
I	Appearance	'Always do p'	Batesian mimics; butterflies with false head; plants which mimic	Not possible
II	Coordination of perception and action	'Do p given that q is so'	Firefly *femmes fatales*; birds which feign injury; angler-fish which darts lure	Males which respond to *femmes fatales* fireflies
III	Learning	'Do any p given that p resulted in q in your past'	Birds of Beau Geste hypothesis; dog which fakes a broken leg	Blue Jays which respond to Batesian mimicry of butterfly; foxes which respond to injury-feigning of birds
IV	Planning	Self-programmed	Chimp which misleads about location of food; humans who lie	Humans deceived by verbal lie

Portia's aggressive-mimicry signalling is another clear example of deception based on coordination of perception and action (Table 14.3).

Arthropod examples of Level III deception, where use of a deceptive ploy is based on learning, may be scarce, but *Portia*'s trial-and-error selection of signals appears to be a straightforward example of this. Level IV, deception based on planning ahead, is where cognition most clearly becomes relevant. We have no evidence that *Portia* plans ahead the particular signals it will use in an aggressive-mimicry sequence. Yet, with detouring, planning ahead is often a component of *Portia*'s prey-capture strategy.

Design options for animal brains

In what was freely admitted to be an 'outrageously oversimplified' framework, Dennett (1995, 1996) considered the basic methods by which animals might solve problems and specified four types of creatures: Darwinian, Skinnerian, Popperian and Gregorian. It may be instructive to consider *Portia* from the perspective of this framework.

Darwinian creatures come with preprogrammed (by natural selection) solutions to particular problems. *Portia*'s preprogrammed tactics for capturing certain of its common prey would appear to fit into this category. Natural selection can be viewed as a trial-and-error process (an algorithm) stretched over evolutionary time, those genotypes that code for successful solutions for problems persisting and those genotypes coding for the unsuccessful being filtered out. Skinnerian creatures do the trial and error within their individual lifetimes, and *Portia*'s trial-and-error tactic appears to be a spider example of this.

It is with Popperian creatures that cognition may become especially pronounced, and it is to vertebrates that we probably most often turn for examples. Unlike a merely Skinnerian creature that must try out a behavior to obtain feedback regarding success or failure, a Popperian creature might be envisaged as running a simulation in some inner environment (mind?) and planning ahead what to do. In its detouring behavior, *Portia* would seem to be Popperian.

Portia probably is left behind when it comes to the fourth type of creature, Gregorian. The Gregorian creature benefits from the problem-solving of others by importing mind tools (e.g. verbal language) from the cultural environment. Perhaps it takes more brain power to become a Gregorian animal than is feasible for *Portia*.

When we began research on *Portia*, few thoughts would have seemed more foreign to us than that one day we would seriously be discussing cognition in a spider. Yet, over and over again, *Portia* has defied the popular image of spiders as simple animals with rigid behavior. One of the challenges in this work has now become to clarify where the limits lie in *Portia*'s cognitive ability, but the greater challenge is to understand how it is that an animal with so little in the way of a brain can nevertheless do so much.

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