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The Cognitive Animal

Empirical and Theoretical Perspectives on Animal Cognition

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In an emerald rainforest of northeastern Australia, a sunbeam pierces the canopy, touches broad green leaves on the way down, and beams onto a lichen-spotted rock surface. In the beam's circle, the slow, careful motions of a brownish jumping spider are illuminated. The jumping spider belongs to the genus *Portia* and it is stalking its prey, a different species of spider sitting in its own web. *Portia* steps cautiously from the rock surface out onto the web and stops. Delicately, *Portia* begins to pluck the web with its palps and legs, making signals that mimic the struggles of a trapped insect. When the prey spider ignores *Portia*'s plucking, *Portia* varies the characteristics of the signals, generating a kaleidoscopic of what appears to be a random selection of signals. Eventually, in response to one of these signals, the prey spider swivels toward *Portia*. Immediately, *Portia* backtracks to that particular signal and repeats it again and again. There being no further response from the prey, *Portia* eventually reverts to broadcasting a kaleidoscope of signals. When the prey spider still moves no farther, *Portia* adopts another ploy.

Now *Portia* slowly and carefully stalks across the web toward the resident spider, intermittently making a variety of signals. From time to time, a soft breeze blows, ruffling the web. The ruffling creates background noise in the web, and *Portia* exploits these moments, during which the resident spider's ability to detect an intruder is impaired, by stalking faster and farther during these periods than when the air is still. Nearing the resident spider, *Portia* makes a signal that elicits from the resident spider a sudden, rapid approach. However, the spider advances very aggressively, and *Portia* scrambles to the edge of the web, then turns around to look over the scene. Soon *Portia* moves away from the web and undertakes a lengthy detour, first going away from the prey and around a large projection on the rock surface, losing sight of the prey spider along the way.

About an hour later, *Portia* appears again, but now is positioned above the web on a small overhanging portion of the rock. After anchoring itself to the rock with a silk dragline, *Portia* next slowly lowers itself down though the air, not touching the web at all. Arriving level with the resident spider, *Portia* suddenly swings in, grabs hold of the unsuspecting spider, and sinks its poison-injecting fangs into the hapless victim. So ends another spider-eat-spider episode from the rainforest; it is typical of hundreds that we have witnessed in the field and raises interesting questions about spider cognition. In the discussion to follow, we will return repeatedly to this hunting example.

When we began studying the species of *Portia* about 20 years ago, little was known about the behavior of these unusual tropical members of the spider family Salticidae (jumping spiders or salticids for short). About two dozen species of *Portia* have been described. They are distributed from Australia through the Indonesian and Malaysian island chains into China, the Indian subcontinent, and Africa. The adults tend to be 8–12 mm in body length and live in habitats ranging from low-elevation rainforest to montane pine forests to savannah.

Across all habitats, whenever *Portia* has been studied, it has been shown to specialize on other spiders as prey, invade webs, and practice aggressive mimicry (Jackson and Wilcox 1998). All *Portia* also build their own webs, which they use for capturing both insects and spiders. Web-based behavior is unexpected in a salticid. Typical salticids neither build nor invade webs. Instead, they use their acute eyesight to guide stalk-and-leap sequences on insects carried out on the ground, on tree trunks, and in foliage (Jackson and Pollard 1996). Remarkably, *Portia* also practices away-from-webs stalk-and-leap sequences. Being highly effective at capturing prey in each setting (away from webs, in its own web, and in another spider's web), among salt-

icids *Portia* is a jack of all trades and the master of them all (Jackson and Hallas 1986).

It is the intricate details of web invasion and aggressive mimicry that especially raise questions about cognition. Web-building spiders from families other than salticids have simple eyes and only poor eyesight (Land 1985). Web signals (i.e., the tension and movement patterns of silk threads) can be envisaged as the language of the typical web-building spider (Foelix 1996). When *Portia* enters an alien web, it manipulates the silk, making web signals that deceive and control the behavior of the resident spider. Simply overpowering the resident spider with strength and speed would not appear to be an option for *Portia*. A spider's web is extremely sensitive to encounters with objects of *Portia*'s size, making undetected web entry exceedingly difficult. Making matters worse, the resident spider is also a predator. There is a serious potential for the tables to be turned. Preying on other spiders is a game where *Portia* may pay for mistakes with its life (Jackson and Wilcox 1998).

That *Portia* might use aggressive mimicry to prey effectively on one or a few types of web-building spiders would have been an interesting finding, but what we found was unexpected. *Portia* is highly effective at taking almost *any kind* of web-building spider. Not only are virtually all the web builders in its natural habitat taken, but in the laboratory, on first exposure, *Portia* routinely makes effective use of aggressive mimicry to control the behavior of, and prey upon, spiders it would never have encountered in its evolutionary history (Jackson and Wilcox 1993a). One of our initial objectives was to understand the basis for this exceptional flexibility.

Devising a method for studying *Portia*'s signals became a critical requirement. For fine-grained detail, this can be done using laser recording technology (Tarsitano et al. 2000). For routine work, however, we devised a home-grown, computerized system for recording, analyzing, and playing back signals (Wilcox and Jackson 1998). We recorded signals with a gal-

vanometer connected by its stylus to the web, coded the very low-frequency signals with a frequency modulation (FM) coder, and stored the coded signals on the soundtrack of a videotape, while simultaneously recording by camera the behavior sequence being observed. Decoded FM signals were converted to digital form when they were input into a laptop computer. The computer was used to analyze the signals for frequency, length, and other characteristics. Signals were played back by making a tiny magnet oscillate. This was achieved by amplifying a signal played by the computer into a coil of magnet wire. When the magnet was glued to an object we wished to vibrate, we played an amplified signal into the coil, which made the magnet oscillate in concert with the electromagnetic waves (Wilcox and Kashinsky 1980).

Unlike the resident spider, *Portia* can see shape and form, and we know from experiments that *Portia* sometimes distinguishes the type of prey it has encountered before web contact, thereby being able to make appropriate adjustments in its mode of approach. For example, there is a Philippine population of *Portia* living in a habitat where an especially dangerous prey spider is common, a spitting spider that is itself a specialist at feeding on salticids. Upon seeing a spitting spider, these Philippine *Portia* (but not *Portia* from other habitats) consistently approach from the rear. Typically this requires a detour. That this inclination to approach from behind is innate (i.e., does not require prior experience with spitting spiders) was shown by testing *Portia* individuals reared in the laboratory (Jackson et al. 1998).

In *Portia*'s signal-making behavior, there is also evidence of adaptation to particular prey species. For example, after contacting the web, the Philippine *Portia* tends to make only faint signals that fail to provoke a full-scale spitting attack (Jackson et al. 1998). In encounters with the females of certain species of prey, the Australia rainforest *Portia* may begin by making signals that simulate the courtship signals of the

males of the resident spider (e.g., Jackson and Wilcox 1990). On the whole, if the predatory sequence is short, signal generation may appear more or less stereotyped. However, most predatory sequences are lengthy. It is routine in lengthy sequences for *Portia* eventually to broadcast a kaleidoscope of signals until some particular signal “works,” i.e., elicits an appropriate response from *Portia*’s viewpoint. *Portia* then repeats over and over the signal that worked. If it ceases to work, eventually *Portia* may switch back to broadcasting a kaleidoscope. This flexible problem-solving behavior is known as the trial-and-error tactic (Jackson and Wilcox 1993a), and it appears to have a central role in almost all of *Portia*’s signal-making sequences. Thus biases toward particular signals with particular types of prey serve primarily to get a sequence off to a good start, with trial and error being used to finish the job (Jackson and Wilcox 1998).

We have demonstrated experimentally that *Portia* derives signals by trial and error. We successfully encouraged *Portia* to repeat signals we chose at random for reinforcement, where reinforcement might be the spider approaching *Portia* or localized movement of a spider that remained in one place. The coil-and-magnet system gave us control over the prey’s behavior and enabled us to provide these kinds of reinforcement (Jackson and Wilcox 1993a).

Portia’s trial-and-error tactic might be viewed as at least a rudimentary example of a spider thinking, or more technically, spider cognition. A discussion of animal cognition often seems like a walk through a minefield, there being almost as many definitions of cognition as there have been authors discussing the topic. A more rewarding approach is to apply frameworks that raise questions about cognitive processes. For example, Dukas and Real (1993) based a framework on six cognitive properties, which we list here along with a rough, informal indication of what each means in everyday terms: reception (taking in information), attention (focusing on particular tasks), representation (maintaining a mental im-

age or cognitive map), memory (retaining information), problem solving (deriving pathways to the achievement of goals), and communication language (influencing other individuals by manipulating symbols). This framework directs interest toward understanding processes that underpin cognitive phenomena, and the thorny problem of defining cognition in any rigorous way is sidestepped, the rationale being that once we understand the underlying processes, worrying about a global definition of cognition becomes irrelevant (see Dennett 1991).

Returning to our hunting example, although *Portia* makes use of tactile and chemical cues when hunting, *Portia*’s acute eyesight seems to be the most critical factor in making predatory decisions that are interesting to discuss in a cognitive framework. *Portia*’s forward-facing anterior medial eyes support a spatial acuity exceeding that known for any other animal of comparable size, rivaling that of much larger animals such as cephalopod mollusks and primates (Land 1985; Harland et al. 1999). The eyes of *Portia* and other salticids are unique and complex evolutionary solutions to the problem of how to see shape and form using drastically fewer receptors than are present in the eyes of cephalopods, birds, and mammals (Land 1974). The human eye, for example, has over 100 million receptors, but the salticid eye has only 10,000 to 100,000 (Land 1985).

We know a great deal about how salticid eyes achieve exceptional acuity, despite their small size, because of extensive research over the past 80 years. The pioneering work of Homann (1928) was significantly extended by Michael Land’s work on *Phidippus johnsoni* (Land 1969a, b), a tour de force in small-scale physiological optics, and more recently by the wide-ranging comparative and developmental studies of David Blest (Blest et al. 1990). Salticid research is now at a point where we can begin linking decision-making processes directly to details concerning the information made available by a unique eye (see Harland and Jackson 2000a).

The link between acute vision and cognitive capacities is currently being considered in research on *Portia* (Harland and Jackson 2000b). *Portia's* predatory strategy seems to require especially precise decisions before the spider comes into close proximity to its prey. For this, acute vision would seem to have important inherent advantages. By sight, *Portia* can precisely locate and identify spiders from a distance of 30–40 body lengths away, monitor the spider's orientation and behavior during the course of a predatory sequence, and in general quickly gain critical information for predatory decisions during complex interactions with a dangerous prey (Jackson 1992).

Moving to the next category in the framework of Dukas and Real (1993), the trial-and-error tactic highlights how attention may be critical for *Portia's* success as a predator on other spiders. *Portia's* trial-and-error tactic can be envisaged as at least a rudimentary example of learning (see Staddon 1983), and there has been a tendency to emphasize learning in the literature on animal cognition (see Yoerg 1991). Yet learning in itself may not tell us anything particularly interesting about how animals differ in cognitive capacity because learning of one sort or another appears to be more or less universal within the animal kingdom (Bitterman 1965), and even in single cells (i.e., in single-celled protists and in single cells of multicellular animals; see Staddon 1983).

Portia's trial-and-error tactic may be more interesting in relation to attention. The relevance of attention is apparent whenever one watches *Portia* hunting. *Portia's* attentive ability is especially dramatic when *Portia* is preying on social spiders, where many potential prey are present simultaneously in close proximity. *Portia* singles out one prey spider, sometimes with other potential prey spiders active close by in the same web (Jackson and Wilcox 1993a). Dynamic fine control of the targeted social spider's behavior is achieved by means of the focused flexibility inherent in use of trial and error. Rather than

emphasizing how learning is implied by this tactic, however, we prefer to emphasize the *unlearning* evidenced when *Portia* reverts to the kaleidoscope of signals once a given signal ceases to elicit an appropriate response. Something like this sort of unlearning may be a precondition for much of what interests us in relation to animal cognition, however cognition might be defined.

There is more to *Portia's* flexibility than just switching signals, however. Going back to our hunting example, we saw *Portia* making decisions concerning whether to go out onto the web, whether to undertake a detour, and so forth. Moving onto another spider's web illustrates especially important constraints on *Portia's* strategy. The other spider is a predator, and the web is more than just an arena in which the resident spider normally takes its prey. It is also a critical component of the web-builder's sensory system (Witt 1975).

To enter another spider's web is almost literally to walk right into the spider's primary sensory organ (Jackson and Pollard 1996). The extreme sensitivity of spider webs to movement and weight (Barth 1982) means that for an animal of *Portia's* size, it is probably not a realistic option to walk softly enough in the web to avoid making a signal that is detectable to the resident spider. What *Portia* does instead is usually to precisely control the nature of the signal going to the resident spider (i.e., practice aggressive mimicry). However, there are times when *Portia* does simply walk across the web, which brings us to the opportunistic smokescreen tactic.

In our hunting example, when the wind created background noise in the web (an opportunistic vibratory "smokescreen"), *Portia* moved faster and farther across the web than when the air was still. We have shown experimentally (Wilcox et al. 1996) that wind and other disturbances (e.g., an insect struggling in the web) make large-scale web signals that mask the fainter signals from *Portia's* footsteps. *Portia* is flexible and takes advantage of these opportunities to move rapidly across the web without

alerting the resident spider. The opportunistic smokescreen tactic also illustrates interesting levels of attention because this tactic is practiced only when *Portia* is approaching a resident spider and not when it is approaching an ensnared insect or an egg sac of the resident (Wilcox et al. 1996).

In our hunting example, the resident spider responded to *Portia*'s signals and rapidly moved toward *Portia*, but the resident approached too fast and *Portia* moved away. When it was at the edge of the web again, *Portia* looked the situation over and made a decision not to reenter the web. Instead, it chose to plan and undertake a detour. The detour ended with *Portia* positioned better than before, ready for an attack where entering the web would not be necessary. *Portia* chose instead to drop on a line of silk parallel to the web and swing in to capture the resident. Detours similar to this have been observed hundreds of times in nature and the laboratory (Jackson and Wilcox 1993b).

There have been extensive experimental studies of *Portia*'s detouring behavior in the laboratory (Tarsitano and Jackson 1992, 1994, 1997; Tarsitano and Andrew 1999) showing, for example, that *Portia* can choose between correct and incorrect pathways leading to a spider lure, and make detours that initially require moving away from the prey, being out of sight of it, and even bypassing an incorrect pathway on the way to choosing the correct one. Other jumping spiders are also known to take detours (Hill 1979), but *Portia* takes detours more readily, takes longer detours, and seems to be unusual in not needing to maintain visual orientation on the prey spider when conducting the detour (Tarsitano and Andrew 1999).

The utilization of planned detours has especially interesting cognitive implications, suggesting the use of mental maps (representation; see Dyer 1998) and prolonged memory. Planned detours (Tarsitano and Jackson 1997) are also interesting as an example of problem solving. The trial-and-error method was also an example

of problem solving, but planned detours differ because the solution is derived before execution of the behavior. Deriving a solution before execution of behavior comes especially close to what would be called "thinking" in lay terms (see Dennett 1996).

What about the sixth category in the framework of Dukas and Real, communication language? The manipulation of symbols with arbitrarily assigned meanings is inherent to verbal language and surely this is beyond anything achievable by a spider brain. Yet the stringing together of signals during aggressive mimicry sequences is at least remotely suggestive of something akin to verbal language. It is a much more dynamic undertaking than we originally appreciated. Calling *Portia*'s signal-making behavior "aggressive mimicry" raises the question of what *Portia* mimics, but this may be less important than trying to understand how *Portia* achieves fine control of its victim's behavior. The emphasis should perhaps be on how *Portia* takes advantage of biases in the victim's nervous system, adopting a perspective akin to recent ideas about receiver psychology (Guilford and Dawkins 1991) and sensory exploitation (Proctor 1992; Ryan and Rand 1993; Clark and Uetz 1993), but with a greater emphasis on complexity, flexibility, and dynamic interaction between signaler and receiver. Studying *Portia*'s signal-making strategy from this perspective may bring us closer than we initially expected to something like the cognitive implications of verbal language.

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