1 *Portia* Perceptions: The *Umwelt* of an Araneophagic Jumping Spider

Duane P. Harland and Robert R. Jackson

The Personality of *Portia*

Spiders are traditionally portrayed as simple, instinct-driven animals (Savory, 1928; Drees, 1952; Bristowe, 1958). Small brain size is perhaps the most compelling reason for expecting so little flexibility from our eight-legged neighbors. Fitting comfortably on the head of a pin, a spider brain seems to vanish into insignificance. Common sense tells us that compared with large-brained mammals, spiders have so little to work with that they must be restricted to a circumscribed set of rigid behaviors, flexibility being a luxury afforded only to those with much larger central nervous systems.

In this chapter we review recent findings on an unusual group of spiders that seem to be arachnid enigmas. In a number of ways the behavior of the araneophagic jumping spiders is more comparable to that of birds and mammals than conventional wisdom would lead us to expect of an arthropod.

The term *araneophagic* refers to these spiders' preference for other spiders as prey, and jumping spider is the common English name for members of the family Salticidae. Although both their common and the scientific Latin names acknowledge their jumping behavior, it is really their unique, complex eyes that set this family of spiders apart from all others. Among spiders (many of which have very poor vision), salticids have eyes that are by far the most specialized for resolving fine spatial detail. We focus here on the most extensively studied genus, *Portia*.

Before we discuss the interrelationship between the salticids' uniquely acute vision, their predatory strategies, and their apparent cognitive abilities, we need to offer some sense of what kind of animal a jumping spider is; to do this, we attempt to offer some insight into what we might call *Portia's* personality. We are able to offer such a perspective because we have been immersed in the natural history of this animal over the course of many years of research. We will try to share our perspective by offering three "stories" from the life of *Portia*.

Portia is a genus containing about twenty species of primarily tropical salticids that are restricted to Africa, Asia, and Australasia (Wanless, 1978). Rain forest is the typical habitat for most of these species, and our stories take place in the rain forest of northeast Queensland, Australia. *Portia*'s microhabitat within the forest is unusual. Salticids are traditionally envisaged as hunters who have little use for webs (Richman and Jackson, 1992). However, *Portia* frequents webs, both self-built and those of other species (Jackson and Blest, 1982a). *Portia* is also unusual in its appearance, both when quiescent and especially when walking.

When seen out of context, for instance on a laboratory table, *Portia*'s walking gait appears overacted, even comical. With its eight legs waving about in a slow, jerky manner, *Portia* is reminiscent of a robot in a 1950s science fiction movie. Under natural circumstances, however, its gait makes sense. *Portia* is a convincing mimic of the detritus found on the forest floor and in webs. Its body is covered with a fine, low-contrast patchwork of browns, softened by fringes of hair. When walking, its exaggerated, hesitating stepping motion preserves its concealment. It appears to be no more than a piece of detritus flickering as dapples of sunlight filter through the canopy (figure 1.1A).

Stalking a Jumping Spider

Our first story begins with *Portia* slowly walking down the trunk of a tree, perhaps looking for the webs of potential prey. As do all salticids, *Portia* trails a line of silk, called a dragline, behind it as it walks (Richman and Jackson, 1992).

Many animals frequent tree trunks in the forest and before long *Portia* steps onto the draglines of another salticid. In this case they are the draglines of *Jacksonoides queenslandicus* (figure 1.1B), the most abundant salticid in the Queensland rain forest (Jackson, 1988), and among *Portia*'s favorite prey (Clark and Jackson, 2000).

Portia is sensitive to the chemical and odor cues from the other spider's draglines (Jackson et al., 2002). These cues prime *Portia* to expect to find *J. queenslandicus* in the vicinity, and the priming actually makes *Portia* more effective at visually locating the prey. When quiescent on a tree trunk, however, *J. queenslandicus's* markings make it hard to see, and this time its camouflage is too good. However, *Portia* has a solution, something called "hunting by speculation" (Clark et al., 2001; see Curio, 1976).

Portia makes a sudden leap straight up into the air. *J. queenslandicus*, resting quietly some 15 cm away, turns to look at what moved, but *Portia* is already back on the ground, sitting still. *J. queenslandicus* does not see *Portia*, but *Portia* detected *J. queenslandicus* as it turned. Very slowly, *Portia* orients toward *J. queenslandicus* and, once *J. queenslandicus* turns away, *Portia* begins to stalk it.

When stalking other kinds of spiders, *Portia* moves slowly, with its palps hanging loosely in front of its face. When stalking a salticid, however, *Portia* moves even more slowly, exaggerating its choppy, robotlike gait, and pulls its palps back so they are hidden from the prey's view (Jackson and Blest, 1982a; Harland and Jackson, 2001).

Being a salticid, *J. queenslandicus* can see well, and this time it detects a flicker of movement as *Portia* comes up from behind, and it turns toward *Portia*. *Portia* freezes the instant its prey's large eyes come into view (Harland and Jackson, 2000a). *J. queenslandicus* looks straight at *Portia*, but sees nothing to indicate danger. Eventually *J. queenslandicus* turns and walks away. With *J. queenslandicus's* eyes no longer in sight, *Portia* resumes its slow advance.

Portia draws steadily closer to its prey, continuously maneuvering to stay behind the *J. queenslandicus*. Eventually, from a few millimeters away, *Portia* lunges, and its fangs pierce the integument just above the brain of the *J. queenslandicus*. The victim is soon paralyzed; *Portia* feeds, and our first story comes to an end.

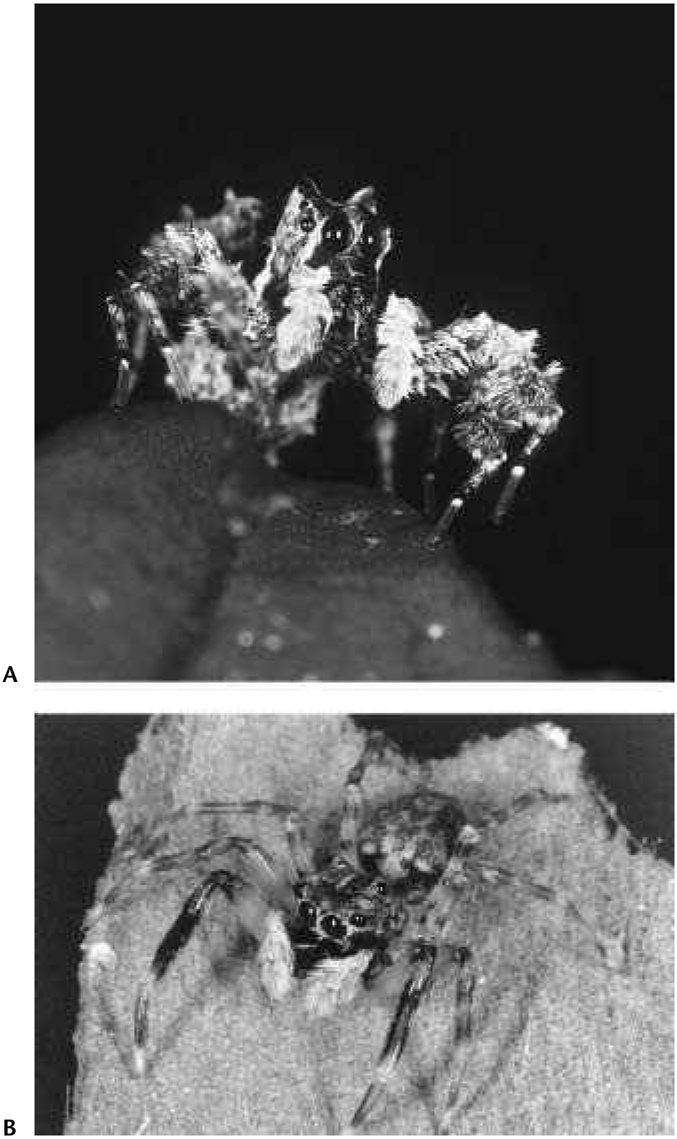

Figure 1.1
(*A*) *Portia fimbriata* subadult male from Queensland, Australia, and (*B*) primary salticid prey of the Queensland *Portia*, the insectivorous *Jacksonoides queenslandicus*. (Photo of *P. fimbriata* by D. Harland; photo of *J. queenslandicus* by R. R. Jackson.)

Deceiving an Orb Weaver

Portia sits near the edge of an orb web, looking across the sticky spirals toward the web's architect, *Gasteracantha* sp., sitting at the hub. *Gasteracantha* is a distinctive spider. It is large, powerful, and has long horny spines on its abdomen that make it difficult for *Portia* to hold on to.

Gasteracantha's eyesight is too poor to recognize *Portia* as a predator. However, *Gasteracantha* has an acute ability to detect and interpret web signals—displacements, even very small displacements, of its web's silk lines (Witt, 1975). *Portia's* task is to get within attacking distance without eliciting the wrong response from *Gasteracantha*. This large spider is fully capable of preying on *Portia* should it get the upper hand. Just walking across the web will not work for *Portia*. The resulting web signals will give it away.

So *Portia* moves slowly onto the edge of the web, reaches out with its forelegs, and begins to pluck on the silk; but *Gasteracantha* does not move. *Portia* continues to make signals, but varies them. It plucks with different legs, plucks with its palps, varies the speed and the amplitude at which its appendages move, and it shakes the web by vibrating its abdomen up and down. Complex patterns are made by simultaneously moving different sets of appendages, with different appendages moving in different ways. By using any combination of its eight legs, two palps, and abdomen, *Portia* is capable of generating an almost unlimited repertoire of web signals.

Eventually a signal may cause a reaction in *Gasteracantha*, and it may approach *Portia*. If the approach is not too fast, *Portia* will continue to signal, slowly drawing the prey spider closer (Jackson and Wilcox, 1993a). *Portia* avoids making web signals that elicit a fast approach because, when moving quickly, *Gasteracantha* is dangerous and more likely to become predator than prey.

Luring *Gasteracantha* is a slow process, and close to an hour has already passed. Then something happens to speed things up. A light tropical breeze gently rocks the web. The wind-induced web movements mask any fainter movements caused by *Portia* and the spider takes advantage of the smoke screen (Wilcox et al., 1996) by stepping rapidly across the web toward *Gasteracantha*. This time, however, when the breeze dies down, *Portia* is still several centimeters from its prey.

Now *Portia* creates a smoke screen of its own (Tarsitano et al., 2000). By violently and repeatedly flexing all of its legs at the same time, the spider shakes the web much as the breeze did. Cloaked by a succession of such diversions, *Portia* closes the remaining distance. However, when it is about 3 mm from *Gasteracantha*, something goes amiss. *Gasteracantha* suddenly turns on *Portia*, lunging forward and grabbing one of *Portia*'s legs with its chelicerae. *Portia* leaps off the web, leaving the leg behind.

After landing on the forest floor half a meter below, *Portia* looks up at the web and then climbs back to it. Once there, it repeats the entire process and this time succeeds in lunging at *Gasteracantha*. *Portia* quickly punctures *Gasteracantha*'s cuticle with its fangs and then lets go. *Gasteracantha* runs to the edge of the web and drops to the ground in an attempt to escape, but paralysis soon sets in. *Portia* drops to the ground on a dragline, walks in the direction of *Gasteracantha*, and scans the forest floor for the specific kind of spider it just attacked (R. R. Jackson, unpublished results). *Portia* will bypass other potential prey placed in its path, continuing to search for the expected prey, in this case, *Gasteracantha*.

Plotting a Detour

Portia walks across the forest floor until its attention is drawn to the distinctive cross-shaped stablimenta adorning the orb web of *Argiope appensa* about a meter away (Seah and Li, 2001). *Portia* moves so that the web is in clear view and approaches the tree to which it is attached. However, the web soon is out of view because of the uneven clutter on the forest floor. The journey to the tree is anything but direct. *Portia* has to continuously change direction along a route that twists around leaves, tree roots, and lumps of dirt. Intermittent visual feedback from the tree and occasionally from the web, combined with an internal sense of direction (see D. E. Hill, 1979), keeps *Portia* on course.

Portia begins climbing the tree toward *Argiope*'s web, but *Argiope* is no ordinary spider. When it detects an intruder on its web, it rocks up and down, shaking the web violently (Jackson et al., 1993). So moving directly onto this spider's web is problematical. One misstep and *Argiope* may shake *Portia* off of the web.

Portia stops just short of the web and slowly looks around. Eventually its line of gaze traces a path (Tarsitano and Andrew, 1999) from the top of the web to a nearby vine and down the vine and into a mass of tangled vegetation adjacent to the tree trunk. *Portia* then turns and walks away, but it is not giving up. Instead, the spider takes a long, convoluted detour, during the course of which it will temporarily lose sight of the web. After about 20 min, *Portia* arrives on the vine it saw above the web. Sitting on a leaf connected to the vine, *Portia* looks down at the resting *Argiope* and lowers itself on a dragline alongside the web without touching it. When it is level with *Argiope*, *Portia* swings in and grabs the unsuspecting prey (see Jackson, 1992a).

The Flexibility of *Portia's* Behavior

Our three stories illustrate a number of examples of behavior which, had they been described in a vertebrate predator, would probably be discussed in the context of animal cognition, animal intelligence, or problem solving. In each of the three cases, the behaviors appear to have a high level of flexibility (or plasticity) for a spider.

Within each story, *Portia* displayed a number of sophisticated behaviors. We focus on three examples, each of which provides some insight into the remarkable sensory capacities of this spider. The behaviors are trial-and-error signal derivation, detouring, and selective attention.

Trial and Error

Although *Portia* is called a specialist because it prefers and is efficient at capturing spiders, the name can be somewhat misleading. That is, *Portia* is actually a generalist on spiders. And, if one considers the variation just in web-building spiders (Jackson and Hallas, 1986a,b), it becomes clear why *Portia*'s behavior needs to be so flexible.

Web-building spiders have only rudimentary eyesight (M. F. Land, 1985a), and so use the information provided by web signals as a primary source of sensory information (Masters et al., 1986; Foelix, 1996). Hence the web itself can be thought of as an integral part of a typical web-builder's sensory system (Witt, 1975).

After entering another spider's web, *Portia* does not approach its victim straightaway. Instead, in an attempt to gain control over its victim's behavior, *Portia* displays a number of aggressive mimicry signals (Jackson and Wilcox, 1998) that the web spider can sense. In the case of its more commonly encountered prey, *Portia* uses specific, inflexible, preprogrammed signals, as one might expect an arthropod predator to do. However, as noted earlier, *Portia* can also create an almost limitless repertoire of web signals by varying the activity of its legs, palps, and abdomen (Jackson and Blest, 1982a; Jackson and Hallas, 1986a). This allows the spider to adjust its web signals in response to feedback from the intended victim (Jackson and Wilcox, 1993a; Jackson and Carter, 2001).

When hunting commonly encountered prey, *Portia* often uses trial-and-error learning to complete a predatory sequence begun with preprogrammed signals (Jackson and Wilcox, 1998). It begins a trial-and-error sequence by presenting the intended prey with a variety of different signals. When a signal elicits an appropriate response, *Portia* stops varying its signals and repeats the successful sequence. If the prey spider stops responding appropriately, *Portia* again generates a variety of signals until one triggers a favorable response from the web's resident, and so on. This appears to be an example of flexible problem solving and represents a rudimentary cognitive ability (see Terrace, 1985; Toates, 1988, 1996).

Altering its web signals through trial-and-error learning enables *Portia* to prey effectively on a wide range of web-building spiders. In the laboratory, this includes species that *Portia* has never encountered in nature and would never have encountered in its evolutionary history.

The convergence of behavioral ecology and cognitive psychology has generated considerable interest in how the cognitive capacities of animals influence their behavior (Yoerg, 1991; Belisle and Cresswell, 1997; Dukas, 1998; Kamil, 1998). When examining this relationship, one key consideration must be the extent to which an animal's cognitive abilities are merely single-purpose adaptations tailored for specific functions rather than broader cognitive capacities (Stephens, 1991; McFarland and Boser, 1993). We are only beginning to understand how often and under what circumstances the evolution of cognitive skills has pushed animals across a threshold, so to speak, enabling them to respond flexibly and adaptively to problems outside of the context in which these skills originally evolved (see Dennett, 1996).

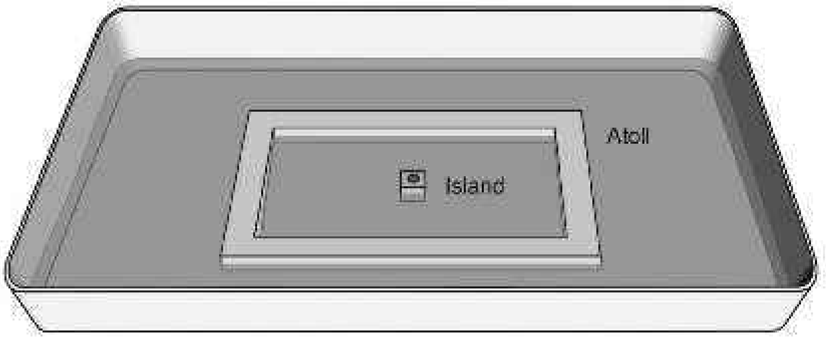

Figure 1.2
Apparatus that was used for ascertaining whether *Portia fimbriata* uses trial and error to solve a confinement problem. The spider is put on a block (island) surrounded by a frame (atoll) in a water-filled tray. It must choose to either leap or swim to reach the atoll and then again choose how it should reach the tray's edge. The successful choice was predetermined randomly. If it was successful, the spider was moved to the atoll; if unsuccessful, it was returned to the island. (Adapted from Jackson et al., 2002.)

Portia may be at this threshold. For instance, we tested *Portia* in a situation in which it had to discover a method of escape through trial and error (Jackson et al., 2001). In the experiments, *Portia* was confined to an artificial island surrounded by water (figure 1.2). This particular problem was chosen because it is unlikely to be similar to anything this spider is likely to encounter in the wild. *Portia* was forced to choose between two potential escape tactics (leap or swim), one of which would fail (it would bring the spider no closer to the edge of the tray) and the other of which would result in partial success (it would bring the spider closer to the edge of the tray). *Portia* consistently repeated choices that brought partial success and avoided choices that brought failure.

Detouring

Although detouring has been most extensively studied in vertebrates (O. von Frisch, 1962; Curio, 1976; Collett, 1982; Chapuis, 1987; Rashotte, 1987; Regolin et al., 1994, 1995a,b), more than 67 years ago Heil (1936) suggested that salticids can make deliberate detours. This was subsequently confirmed experimentally by D. E. Hill (1979) using a North American species of *Phidippus*. The detours required in Heil's and Hill's experiments were simple and short, and Hill (1979) concluded that detouring required no insight because, in the absence of a straight path to the prey, all the salticid did was to head toward an object ("secondary goal") that would bring it closer to the prey (the "primary goal"), and it continued doing this until the prey was reached. Hill's (1979) conclusion, however, does not appear to apply to *Portia*.

Portia reaches its prey by taking indirect routes (detours) when direct routes are unavailable (Tarsitano and Jackson, 1992; Tarsitano and Andrew, 1999), including detours that can be completed only by initially moving away from, and losing sight of, the prey (reverse-route detours) (Tarsitano and Jackson, 1994, 1997). In encounters with certain types of prey, such as spitting spiders, which are particularly dangerous (D. Li et al., 1999), *Portia* takes detours even when shorter, direct routes are available (Jackson and Wilcox, 1993b; Jackson et al., 1998). Solving path-finding problems by selecting a route ahead of time (Tarsitano and Jackson, 1997) implies planning ahead (i.e., a type of offline processing; see Toates, 1996), a putative cognitive ability when it is manifested by vertebrates.

Selective Attention

Chemical cues from *J. queenslandicus* have been shown experimentally to facilitate the speed with which *P. fimbriata* attend to visual cues from *J. queenslandicus*. These findings appear to be an example of attentional priming (see Roitblat, 1987). This is noteworthy in that chemosensory stimuli are priming responses to visual stimuli and because this appears to be an instance in which the priming mechanism appears to be preprogrammed.

Attentional priming, in conjunction with *Portia's* apparent use of search images (as noted earlier; L. Tinbergen, 1960; Bond, 1983; Langley et al., 1996), suggests that this spider can access a mental representation of an unseen but expected prey item. However, what "representation" might mean for *Portia* is unclear (see Roitblat, 1982; Epstein, 1982). In perhaps the simplest case, attentional priming might be explained by a direct chemosensory-induced increase in the sensitivity of a single hypothetical feature-detecting neuron in *Portia*'s visual system. Further research on the mechanisms behind *Portia*'s visual perception is needed.

Integrating Tactics

During much of the twentieth century, the prevailing assumption was that arthropod behavior is rigid, and researchers often expressed surprise at how varied a salticid's responses could be. For instance, Homann (1928) noted that individual spiders with the same eye experimentally occluded occasionally acted differently from one another. Crane (1949) tried to account for her spiders' behavioral variability by hypothesizing the existence of "epigamic rhythms" and short-term cyclical fluctuations of internal state. In a series of careful experiments on color discrimination, Kästner (1950) tested the salticid, *Evarcha fulcata* (Clerck), and found it preferred a striped over a uniformly colored target of identical brightness. However, during retests, many spiders switched preferences (despite the fact that neither target offered a reward or escape option). This behavior was so unexpected that Kästner admitted simply that it was impossible for him to explain these facts.

Variability is a dominant theme in *Portia*'s behavior, seeming to highlight the flexibility of its prey-capture strategy. During predatory encounters, *Portia* rarely relies exclusively on any one tactic. Instead, it switches between or combines tactics, often appearing to derive a unique solution for how to capture a particular prey spider under a particular set of circumstances.

The Evolution of Behavioral Flexibility in *Portia*

Theoretical accounts of the evolution of *Portia's* problem-solving ability have emphasized the close relationship between this spider's behavior and its prey's sensory systems, the high level of risk involved in attempting to gain control over another predator's behavior, and the potential for co-evolution between predator and prey (Jackson, 1992a).

Limits of scale must place a ceiling on how flexible an animal's behavior can become, but how and where size constraints become important remain unresolved questions. Smaller animals tend to have fewer, not smaller, neurons (Alloway, 1972; Menzel et al., 1984), which means fewer components are available for brains, sensory organs, problem-solving mechanisms, and cognitive and behavioral flexibility. There is considerable evidence that even over a small size range and among closely related species, brain size influences cognitive capacities (Lashley, 1949; Rensch, 1956; Jerison, 1973, 1985; Eisenberg and Wilson, 1978; Clutton-Brock and Harvey, 1980; Mace et al., 1981; Lefebre et al., 1997). Hence, small brain size seems to present a fundamental engineering problem that potentially limits how complex or flexible an arthropod's behavior can become (Harland and Jackson, 2000b). On the other hand, *Portia's* behavior suggests that the chasm between small-brained and large-brained animals may not be quite as enormous as has been conventionally thought (see Bitterman, 1986). The key to understanding *Portia*'s remarkable behavior may lie in its unusually complex sensory systems, especially its vision.

Salticid Sensory Systems

Nonvisual Senses

Vision has been considered to be essential to the behavior of salticids (Drees, 1952; M. F. Land, 1969a,b). Hence, research on salticid sensory systems has focused almost exclusively on their unique eyes. Thus what is known about their other sensory capacities is limited. However, behavioral observations indicate that salticids may rely heavily on modalities other than vision. For instance, when they are in complete darkness, some salticids readily use substrate-borne vibratory signals during mating (Taylor and Jackson, 1999). Most salticids can capture prey in total darkness (Taylor et al., 1998), and *Portia* can invade webs and use web signals in the dark (R. R. Jackson and D. P. Harland, unpublished results).

Chemoreception is also important to *Portia* (Peckham and Peckham, 1887; Heil, 1936); pheromones left by conspecifics influence courtship (Pollard et al., 1987). Furthermore, *Portia* can discriminate between itself and conspecifics, identify conspecifics as familiar, and determine the sex of conspecifics based on chemical cues imbedded in their silk (Willey and Jackson, 1993; R. J. Clark and Jackson, 1994a,b, 1995a,b). Air- and substrate-borne chemical cues are also used to detect commonly encountered prey (Jackson et al., 2002).

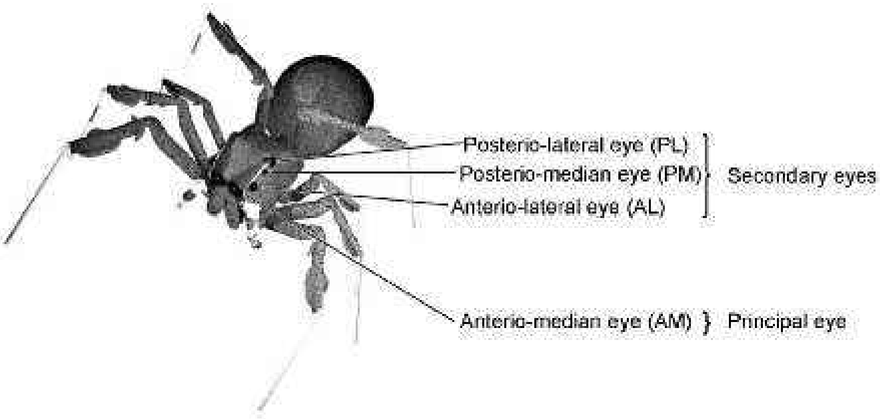

Figure 1.3
Drawing of *Portia fimbriata* showing the external arrangement of salticid eyes. The principal (AM) eyes function in high-acuity and color vision. The secondary eyes (PL, PM, AL) function in motion detection.

Although detailed studies of salticid mechanical senses are lacking, this modality is well described for other spider families (see Foelix, 1996). In other spiders, various mechanosensors (primarily in the form of sensory hairs and slits in the integument) mediate detection of air movement (Barth et al., 1993), deformation of the exoskeleton (Barth, 1985), temperature and humidity (Ehn and Tichy, 1994), and position of the appendages relative to the body (Seyfarth, 1985). It can be presumed that these sensory structures are also present in salticids, but more research is clearly needed.

Vision

In contrast to an insect's pair of multifaceted, compound eyes, salticids have eight camera-type eyes spaced around the cephalothorax (i.e., the frontmost segment of the body) (M. F. Land, 1985a). Acting together, these eyes (figure 1.3) serve much the same role as do the two eyes of a predatory mammal such as a lion. As in mammals, when small-field movement is detected, *Portia* will orient toward it. Once located, the object may be visually tracked, and its identity, size, range, orientation and behavior assessed (M. F. Land, 1974). However, there are important differences in how mammalian and salticid eyes perform these tasks.

In salticids there are two types of eyes, secondary and primary, or principal, eyes. The six secondary eyes, spaced along the sides of the carapace, detect movement in the periphery and enable the spider to orient toward its source. Hence the secondary eyes are functionally analogous to the peripheral retina in vertebrates. The salticid's two principal, forward-facing eyes are larger than its secondary eyes and provide detailed information about the objects toward which the spider is oriented (e.g., the object's shape, texture, and color). This is functionally similar to the mammalian fovea; that is, spatial acuity (the ability to resolve detail) is especially good in the mammalian fovea and, in the salticid, in the central region of the retina of the principal eye.

This division of functions (detection of peripheral movement and assessment of detail) into two types of eyes appears to be an evolutionary response to the limitations of size. For example, transposing the equivalent of a spherical vertebrate eye into a salticid's body would not be a workable option because an eye's optical performance is critically tied to the ratio between the diameter of the lens (aperture) and its ability to magnify (focal length) (M. F. Land, 1974, 1981; Land and Nilsson, 2002). The degree of magnification provided by a lens determines how far behind the lens an image will form, and increasing the magnification means increasing the distance between the lens and an image. If we were to design a spherical eye with a corneal lens, and an aperture and magnifying power (focal length) equal to that of the salticid's principal eye, it would have a diameter equal to the length of one of the salticid's principal eyes. The additional volume of the eye (approximately 27 times more) would mean that the single spherical, mammalian-type eye would entirely fill the salticid's cephalothorax (figure 1.4). The salticid's solution to this size-constraint problem has been to divide visual tasks between two types of eyes.

In terms of simple visual resolution, *Portia* has no rival among insects (figure 1.5). For instance, the dragonfly, *Sympetrum striolatus*, has the highest known acuity among insects (i.e., a resolving power of 0.4 deg) (Labhart and Nielsson, 1995; M. F. Land, 1997). In contrast, the acuity of *Portia*'s principal eyes is 0.04 deg, exceeding that of the dragonfly by tenfold despite the fact that dragonfly compound eyes are about the size of *Portia*'s entire cephalothorax (D. S. Williams and McIntyre, 1980)! It is interesting that the human eye, with an acuity of 0.007 deg, is only five times better than *Portia*'s (e.g., M. F. Land, 1981; M. F. Land and Nilsson, 2002).

The Secondary Eyes

The salticid's six secondary eyes are smaller than the two principal eyes (figures 1.3 and 1.4A), but each secondary eye covers a much wider field of view than the principal eyes (figure 1.6). The posterior median (PM) eyes of most salticids are regarded as vestigial because they have degenerated retinas incapable of detecting movement (Eakin and Brandenburger, 1971; M. F. Land, 1985a) (figure 1.6A). Degenerated PM eyes are thought to be a derived condition (Wanless, 1984). For instance, a number of genera in the "primitive" salticid subfamilies Lyssomaninae and Spartaeinae have large functioning PM eyes. (*Portia*, for example, is a spartaeine genus with functional PM eyes; figures 1.4A and 6B). In species with degenerated PM eyes, the fields of view of the remaining secondary eyes have apparently widened (figure 6A) so that they encompass the fields that would be covered by functional PM eyes (M. F. Land, 1985b).

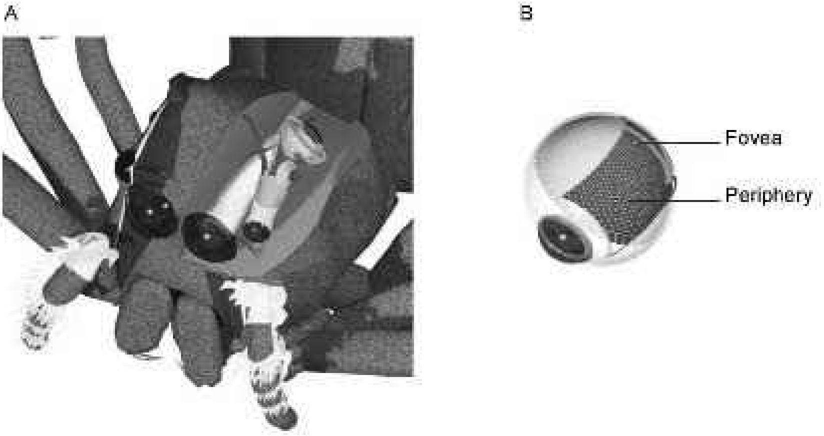

Figure 1.4
Drawing of *Portia fimbriata* showing internal arrangement of salticid eyes. (*A*) Cutaway carapace showing long eye tube of the large, forward facing principal anterior median (AM) eye and compact eye cups of secondary anterior lateral (AL) posterior median (PM), and posterior lateral (PL) eyes (see figure 1.3). Structural tissue (e.g., eye tubes) is shown in gray, retinae in red, and muscles in blue (only the principal eye has muscles). (*B*) A mammalian-type spherical eye (at the same scale and the same viewing angle as in (*A*) that would be needed to incorporate the four salticid eyes into a single eye. To retain a focal length equivalent to that of an anterior median eye, the spherical eye's diameter would have to be the same as the length of the anterior median eye tube. Additional space would be required for muscles (not shown). *P. fimbriata*'s cephalothorax would be filled with a single eye of these dimensions.

Internally, each secondary eye has a regular mosaic of well-separated receptors that form a bowl-like retina. The retina is made up primarily of three cell types: sensory cells, nonpigmented supportive cells, and pigmented supportive cells (Eakin and Brandenburger, 1971). Rhodopsins, embedded in the plasma membranes of sensory cells, detect light. Membranes containing the rhodopsin are highly folded and situated in arrays of slender microvilli (rhabdomeres) held perpendicular to the surface of the retina and the path of incoming light. The section of the sensory cell containing the rhabdomeres is called a rhabdom. Each receptor (an independent functional unit of reception) in the secondary eye is made up of two contiguous rhabdoms surrounded by accessory cells (Blest, 1985a).

The focal lengths for secondary eyes are small compared with the principal eyes, but small focal lengths help provide the secondary eyes with wide fields of view and large depths of field (i.e., there is a large distance over which an image remains in focus).

The role of the secondary eyes as motion detectors is clearly suggested by the heavily pigmented accessory cells between the receptors, which protect and

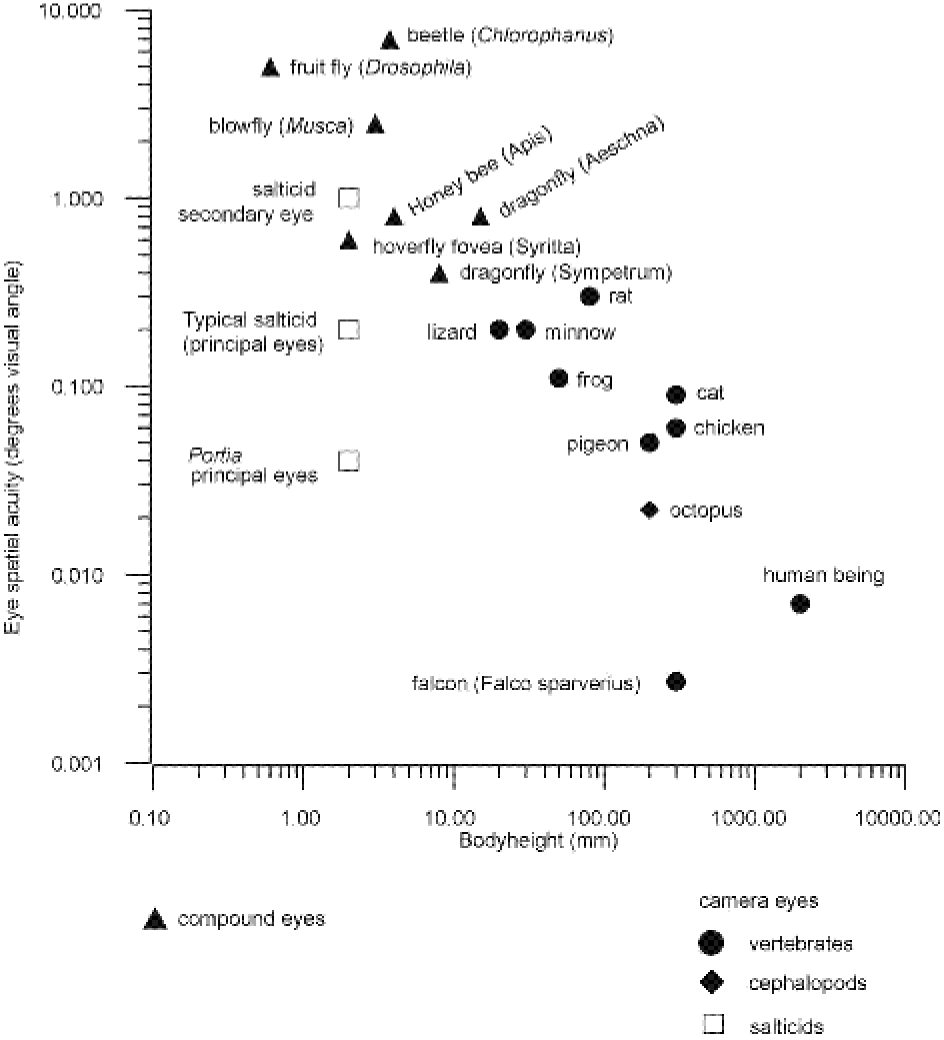

Figure 1.5
The spatial acuity of *Portia*'s eyes compared with that of other animals. The log of spatial acuity (expressed as a minimum interreceptor angle) is plotted against the log of body height. Data from Kirschfeld (1976), M. F. Land (1985a, 1997), and A. W. Snyder and Miller (1978). (Adapted from Kirschfeld, 1976.)

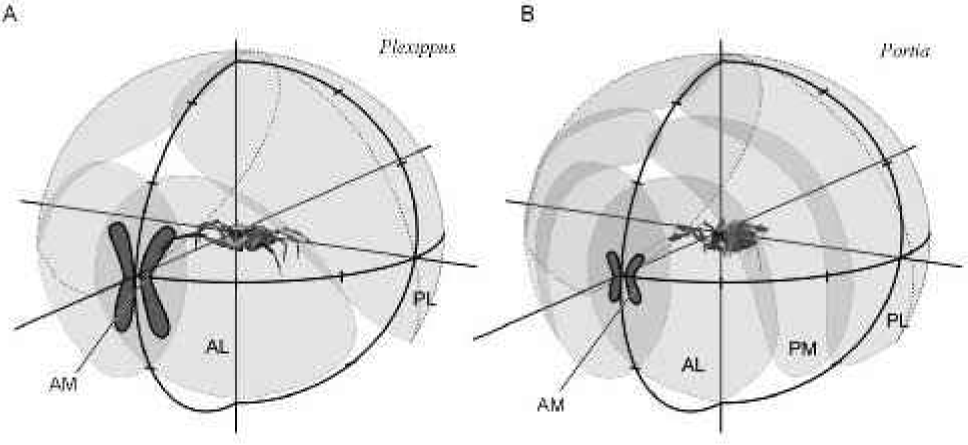

Figure 1.6
Fields of view of the eyes of (*A*) *Plexippus* sp., an advanced salticid (subfamily Salticinae) with vestigial posterior median eyes, and of (*B*) *Portia fimbriata*, a spartaeine (primitive subfamily) salticid that has large functional positerior median eyes. Overlapping visual fields indicate binocular visual fields. The orthographic view is taken from 30 deg longitude and 15 deg latitude. AM, anterior median; AL, anterior lateral; PM, posterior median; and PL, posterior lateral eye. (Adapted from M. F. Land, 1985b.)

help to isolate them optically (i.e., from the effects of stray photons) (Eakin and Brandenburger, 1971; Blest, 1985a). Furthermore, compared with receptors in the principal eyes, those of the secondary eyes tend to be larger, surrounded by supportive cells (Blest, 1983), and widely spaced.

Interreceptor spacing and receptor width are critical factors defining the degree of an eye's spatial acuity. As an image falls on the retina, it is sampled by the receptors, each receptor sampling a specific small area. Put simply, the denser the array of visual sampling units, the higher the degree of spatial detail that can be resolved. Gaps between receptors (as seen in the secondary eyes) also influence acuity by corresponding to gaps in the sampling space. An eye's spatial acuity, expressed as "visual angle" (defined as the degrees apart objects in a scene must be before they are seen as separate), is calculated from the image's quality and spread, which are determined by the aperture and focal length of the lens, plus interreceptor spacing. With visual angles varying between 0.4 and 2 deg, the spatial acuity of salticid secondary eyes tends to be comparable to that of the compound eyes of insects (M. F. Land, 1985a, 1997).

Salticids detect movement when sequential changes in image intensity stimulate adjacent receptors in the secondary eyes (M. F. Land, 1971). A stimulus change between just two adjacent receptors is enough to elicit an orientation response. For example, a small spider walking along the ground to the side of *Portia* might project an image on the posterior lateral (PL) retina that covers a single receptor. As the spider moves, its image will move from one receptor to the next on the PL retina, alerting *Portia* to the presence of a moving object.

The readiness with which a single receptor in the secondary eyes can detect an object is influenced by the size of the object's retinal image, which is a product of the object's absolute size and distance (the nearer the object, the larger its retinal image). For example, Land (1971) found that individual receptors from the PL eyes of *Metaphidippus aeneolus*, with receptive fields of 1 deg, responded to objects with retinal images wider than 0.4 deg (i.e., just less than half a receptor might be covered by the image). The probability of a response increased with the width and height of the stimulus, leveling out for stimuli larger than ~1.1 deg.

The salticid secondary eyes are monochromatic; they contain just one type of rhodopsin, with a maximum sensitivity at 535 nm (our green) (Yamashita and Tateda, 1976; Hardie and Duelli, 1978). In practical terms, this means that a salticid can detect movement of an object when there is a strong contrast in green: either a green object against a background of other colors or an object that is not green moving against a green background. For example, a green dot moving on a black background (or vice versa) provides a high level of contrast and is easily seen by a salticid. However, a red dot moving on a black background is unlikely to be detected.

When movement is detected, a salticid may orient toward the object, bringing it into its principal eyes' field of vision. Information from the secondary eyes governs orienting, which appears to depend on translating the position of stimulation on one of the secondary eye retinas into a particular number of steps by the legs, with legs on opposite sides of the body moving in opposite directions, which turns the spider a specific number of degrees to the left or right (M. F. Land, 1972).

When discussing algorithms that control orientation by animals, a distinction is commonly made between closed- and open-loop turns (Mittelstaedt, 1962; M. F. Land, 1971). Closed-loop turns require that the animal receive visual feedback from its own movement (i.e., the animal continually monitors the object's position). For this, the movement source must remain visible throughout the execution of the turn. In contrast, an open-loop turn is not governed by feedback (i.e., open-loop turns work on a single instruction). For example, movement detected 80 deg to the animal's left can be envisaged as initiating an open-loop algorithm that reads, "turns 80 deg to the left, then stop." A closed-loop algorithm, in contrast, can be envisaged as reading something like "turn a little in the direction of the movement source, after which, if the movement source is in front, stop; otherwise, repeat from the beginning."

An open-loop movement means that if the movement source is removed during the act of orientation, the animal will nevertheless be pointing toward the object's last position at the completion of its turn. Salticids generally orient toward a target in a single turn, suggesting that they rely primarily on an open-loop algorithm. However, turning is occasionally performed as a series of smaller turns, which may mean that they sometimes use a mixture of closed- and open-loop algorithms (M. F. Land, 1971).

Control of orientation toward moving objects is the best known, but not the only, function of the secondary eyes. The interplay of object size, velocity, and movement pattern may be important cues governing different responses. For example, objects that loom up (i.e., suddenly make bigger retinal images) may trigger a "panic" response (Heil, 1936). Furthermore, the speed at which an object moves influences the salticid's reaction. A slowly moving object (e.g., less than 1 deg/s for *M. aeneolus*), generally elicits no response. However, rapidly moving objects (e.g., greater than 100 deg/s for *M. aeneolus*) can provoke a "panic" response if they are large, or a chasing response if they are small (Heil, 1936; Drees, 1952; M. F. Land, 1971; Forster, 1985).

During a "panic" response, a salticid may hide quickly, make a wild leap and then freeze, or simply flee. When fleeing from a predator, salticids appear to use information from the PL eyes to keep a pursuer directly behind them (M. F. Land, 1971).

In contrast, when chasing prey, salticids appear to use information from the anterior lateral (AL) eyes to keep the prey directly in front of them (Drees, 1952; Forster, 1979). Unlike the other secondary eyes, each AL eye contains a forward-facing foveal region with higher spatial acuity (Eakin and Brandenburger, 1971; M. F. Land, 1974). The function of the AL fovea has not been studied, but perhaps it has a role in range-finding or in guiding the principal eyes' saccades.

Range-finding, or distance estimation, is the determination of the distance to an object in the visual field. This ability is important when a salticid is hunting and when it is planning detours. The AL eyes have a forward-facing region of binocular overlap (figure 1.6), which also overlaps the fields of view of each principal anterior median (AM) eye (M. F. Land, 1985b). Experiments in which various eyes were covered with opaque wax or paint suggest that the binocular overlap of the AL eye, in conjunction with the AM-AL overlap, plays a role in range-finding (Homann, 1928; Heil, 1936; Forster, 1979), but the specific contributions of each eye are not well understood.

If distance estimation is restricted to the region of binocular overlap, this may impose a significant constraint on the spider. That is, an object (e.g., an insect) in the lateral visual field may be detected by the secondary eyes, but its distance may undeterminable until it is in the frontal visual field. Suppose, for instance, that a large object (subtending 10 deg) is moving behind the salticid. From the spider's perspective, this could be a small, near object (e.g., insect prey), or a large, distant object (e.g., a predatory bird). An orienting turn might provide an answer, because it would allow the principal eyes to assess the details of the object, but with the risk of scaring off potential prey or falling victim to a predator. Larger turns probably increase the risk of both these outcomes. This may explain why *Portia* and other salticids appear willing to make short turns but reluctant to make larger turns (see M. F. Land, 1971).

The Principal Eyes

For a salticid, as for many vertebrates, orienting toward an object brings a specialized part of the visual system to bear on the target, in the spider's case the retinae of the large anterior median, or principal, eyes (figure 1.3). As indicated earlier, because of their structure, these eyes can provide information that is different from, and more detailed than, that provided by the secondary eyes. Using their AM eyes, salticids can discriminate between at least five broad classes of objects: mates, rivals, prey, predators, and features of the environment (Homann, 1928; Heil, 1936; Crane, 1949; Drees, 1952; Forster, 1979, 1982b). Some of the most basic decisions made by salticids in their day-to-day lives depend on this information. For example, *Portia* plans and executes detours based primarily on optical features of the environment acquired by the AM eyes (Tarsitano and Andrew, 1999). Its choice of signals during an encounter with a web-building spider depends on visually acquired feedback about the identity and behavior of the prey; and *Portia fimbriata* can visually discriminate between prey and conspecifics at distances of up to 46 body lengths (Jackson and Blest, 1982b; Harland et al., 1999).

The AM eyes also make it possible for salticids to identify environmental features in order to navigate detours, and this can be done at distances as far as 85 body lengths (Tarsitano and Jackson, 1997).

The Structure of the AM Eyes On the outside of the salticid's anterior carapace are the large corneal lenses of the principal eyes. In salticids the cornea is formed by the carapace and it is both immobile and nonmalleable. Beyond the surface of the cornea there is a gradient in lens density that corrects the spherical aberration caused by the corneal surface (Blest and M. F. Land, 1977; D. S. Williams and McIntyre, 1980; Forster, 1985; see M. F. Land and Nilsson, 2002).

Despite their large size, the combined fields of view provided by the corneal lenses of the AM eyes are eclipsed by those of the flanking AL eyes (M. F. Land, 1969b, 1985b). This is because the focal length of the AM lens is greater than that of the AL lens. A greater focal length means higher magnification. However, magnification comes at a price. Magnifying an image can be envisaged as spreading the light more thinly over a larger area. Hence, to magnify an image and retain the same brightness, more light is required. The only way to get more light is to make the corneal lens wider. The other consequence of magnifying an image is that the more it is enlarged, the less of it will be in view. In short, by having a longer focal length, the AM eyes have smaller fields of view than the secondary eyes and yet they require larger lenses. Only larger lenses can provide enough light to maintain an acceptable quality for the magnified images.

Behind the AM corneal lens is a long, slightly tapering eye tube (figure 1.7). Transparent glass cells fill all except the rearmost part of the eye tube. After passing through the glass cells, light enters the matrix of cells supporting the retina (Eakin and Brandenburger, 1971). Along the optical axis, the anterior interface of this supportive matrix forms a concave pit just in front of the retina. This pit functions as a diverging lens that magnifies the image from the corneal lens (figure 1.8), boosting the eye's overall focal length. In *P. fimbriata*, the focal length of the corneal lens alone is 1701 μm. With the pit magnifying the image from the corneal lens, the eye acts as a telephoto lens system with a focal length of 1980 μm (D. S. Williams and McIntyre, 1980).

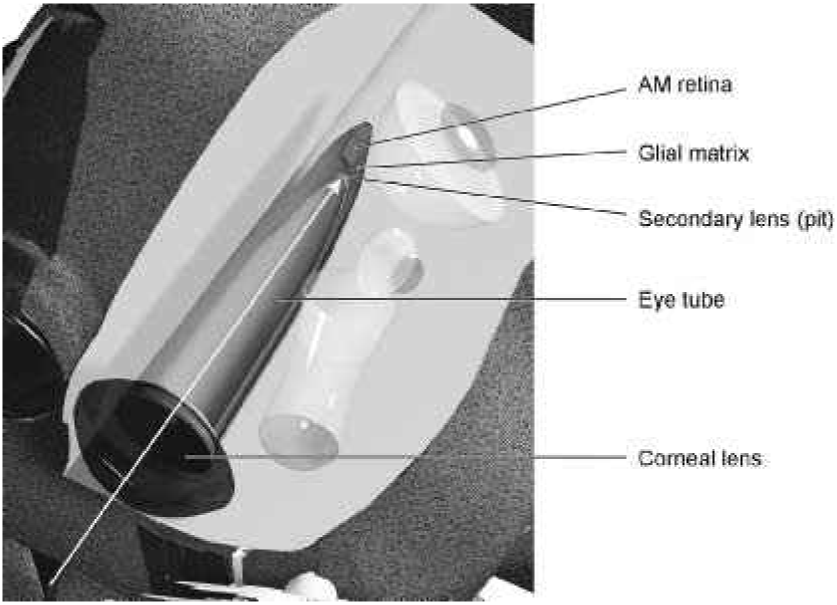

Figure 1.7
Morphology of the anterior median eye of *Portia*. Light (yellow line) enters the eye through the corneal lens and passes down the eye tube (cut along its sagittal plane), which is filled with (low optical density) glass cells. It is then magnified by the secondary lens (pit) formed by the interface with the (high optical density) glial matrix. The images focus within the retina.

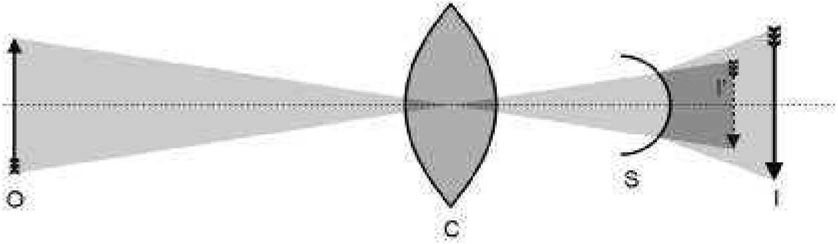

Figure 1.8
Telephoto optics of the salticid principal anterior median eye. The image (I) of an object (O) is projected by the corneal lens (C) onto the retina after being magnified by a secondary (diverging) lens (S) to make an image of size I. I′ shows the approximate size and position of the image without the secondary lens. (Adapted from D. S. Williams and McIntyre, 1980.)

Salticids are not alone in using a diverging lens as a space-saving method of increasing image magnification. The eyes of falconiform birds also have foveal pits that operate as telephoto components, providing these birds with the highest spatial acuity known for any animal (up to 2.6 times greater than our own) (A. W. Snyder and Miller, 1978).

After being magnified by the secondary lens, the image is brought into focus on a complex retina. Unlike our own retina, the photoreceptors in the salticid AM retina are stacked in four successive tiers, or layers, along the light path (figure 1.9; plate 1). To reach the rearmost tier, layer I, light must pass through layers IV, III, and II (M. F. Land, 1969a; Eakin and Brandenburger, 1971; Blest et al., 1981).

Color Vision

The tiered arrangement of the AM retina plays a critical role in color vision. Light is split into a spectrum by the telephoto optics, with different wavelengths coming into focus at different distances. This is known as chromatic aberration (M. F. Land and Nilsson, 2002). Short wavelengths come into focus in layer IV, and longer wavelengths come into focus in layer I. Color vision based on chromatic aberration is effective because the photoreceptors in each layer contain different rhodopsins, each of which is sensitive to the wavelength that comes into focus on that layer (figure 1.10A) (M. F. Land, 1969a; Blest et al., 1981).

Although receptors sensitive to ultraviolet (UV), blue, green, and yellow have been found in the AM retinas of a few salticid species (DeVoe, 1975; Yamashita and Tateda, 1976), receptor location has been determined for just one species. Blest et al. (1981) found that the receptors in layer IV of *Plexippus validus* (Urquhart) have a peak absorbency in the UV range (~360 nm), and that receptors in layers I and II have a peak absorbency at 520 nm (green) (figure 1.10B). Although Blest and colleagues did not succeed in sampling receptors from layer III, optical calculations based on the position of the green and ultraviolet receptors suggest that peak absorbency in blue would enable layer III receptors to receive maximally sharp images. Wavelengths longer than green (e.g., red, ~700 nm) may also be absorbed at low efficiency by the green receptors in layers I and II (Peaslee and Wilson, 1989).

Whether salticids can discriminate light in the green region of the spectrum from light in the red region remains more controversial. Although physiological and optical studies have failed to find convincing evidence of separate green and red receptors, there are reasons to expect that discrimination is possible. In many salticid species, males have distinct red patches in their body patterns that are usually associated with courtship (figure 1.10C; plate 7), and the results of one study (Nakamura and Yamashita, 2000) suggest that salticids can learn to avoid red or green colored paper when that color is associated with heat punishment.

The tiered arrangement of the AM retina makes it tempting to suggest that salticid color vision operates by combining images from the different receptor layers into a single colored picture. However, this is probably not done, given the fact that none of the receptor mosaics match because receptors in different layers along any

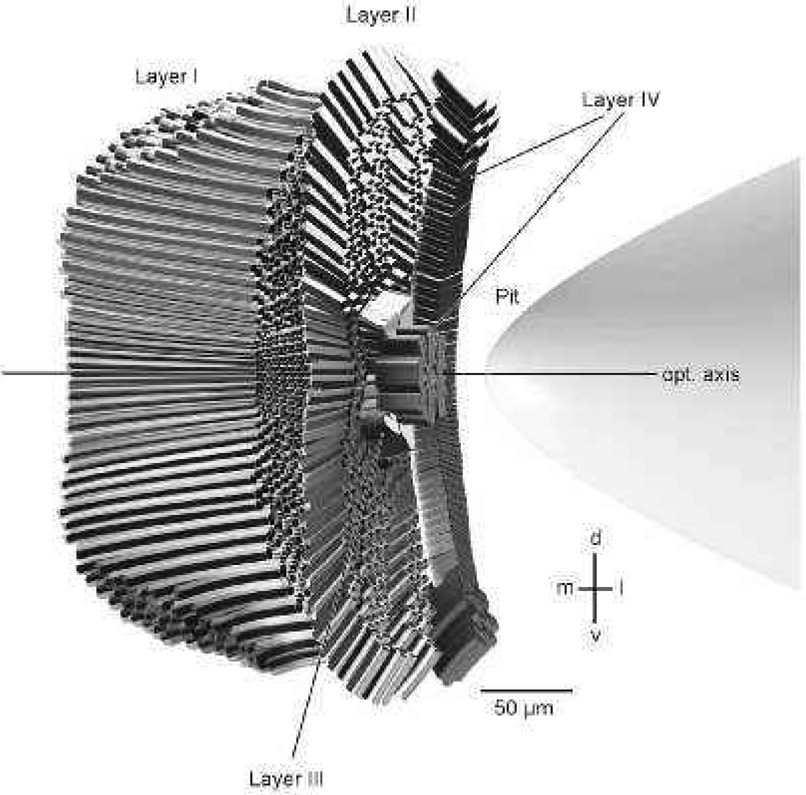

Figure 1.9
Structurally complex retina of *Portia fimbriata*'s principal eye. Behind the pit (secondary lens) are four layers of receptors (I, II, III, and IV) stacked along the optical axis. Layers II, III, and IV contain more than one receptor type. Most receptors are short, with irregular transverse cross-sectional profiles. Layer I is highly ordered with well-separated receptive segments. Separation reduces interreceptor interference. Spatial acuities as low as 2.4 min arc are supported by the central fovea of layer I. The orthographic view is taken 55 deg from the inner side of the optical axis (opt. axis) of the secondary lens. Orientation: d, dorsal; m, medial; l, lateral; v, ventral. Electron micrographs and structural descriptions were used to construct the drawing taken from D. S. Williams and McIntyre (1980), Blest et al. (1981), Blest and Price (1984), and Blest (1987a,b). (See plate 1 for color version.)

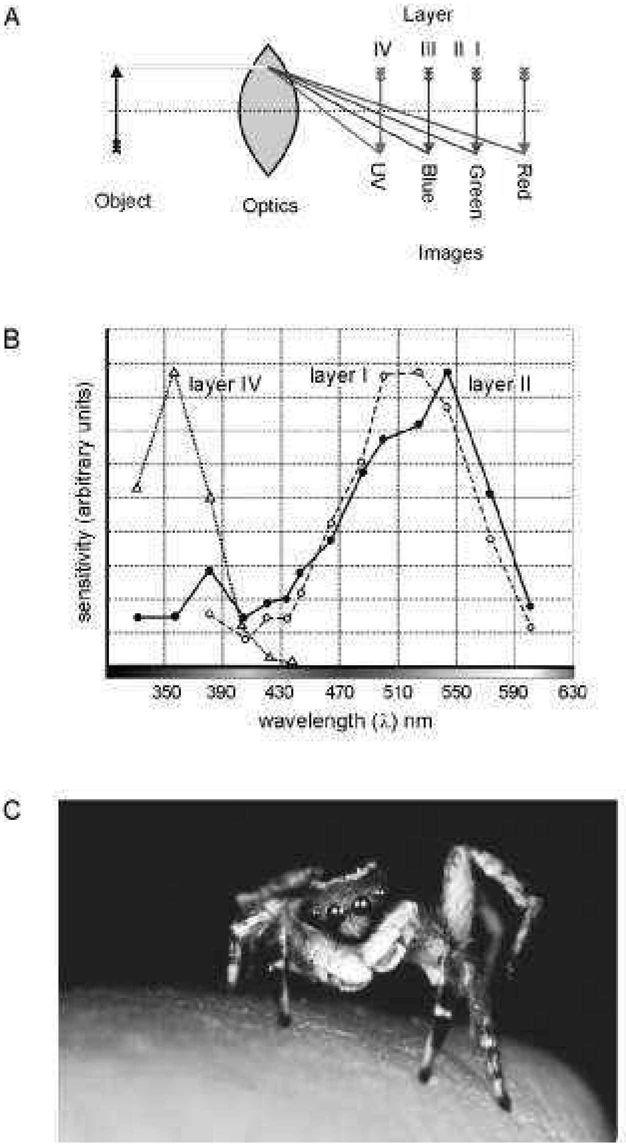

Figure 1.10
Hypothetical mechanism responsible for salticids' color vision. (*A*) Chromatic aberration of the anterior median eye optics is harnessed because green, blue, and ultraviolet (UV) components of an image come into focus on layers I, III, and IV, respectively. (*B*) Spectral sensitivity of marked cells from layers IV, II, and I within the AM eye of *Plexippus validus*. (Adapted from Blest et al., 1981.) (*C*) Undescribed adult male salticid from Sri Lanka showing colored patches associated with courtship, including red patches on the femur of each front pair of legs. (Photo by D. Harland.) (See plate 7 for color version.)

specific light path are of different sizes and shapes. Hence, the salticid cannot derive a color picture simply by combining information in a receptor-for-receptor (or point-for-point) manner. What color means to a salticid is one of the bigger unresolved questions about their vision. Obtaining an understanding of the psychological meaning of color for salticids will be an especially challenging problem for future research.

Possible Functions of the Low-Acuity Layers IV, III, and II

Structural differences in each of the layers suggests that they have functional differences that go beyond color vision. layer IV, the layer with the fewest receptors, is the first layer through which light passes in the AM retina (figure 1.9). This layer has the poorest spatial acuity but the most complex topography (figure 1.11; plate 2) (M. F. Land, 1969a; Eakin and Brandenburger, 1971; Blest et al., 1981; Blest and Price, 1984). A well-organized vertical strip of receptors lies along the outer side of the AM retina (4a), but the mosaic in the middle of the retina (4b) is poorly organized. Poorly organized regions also lie scattered peripherally (4c). The kind of information provided by layer IV is unclear. However, it has been suggested that region 4a detects the polarization plane of ultraviolet light (M. F. Land, 1969a; Eakin and Brandenburger, 1971). In other arthropods (K. von Frisch, 1949; Brines and Gould, 1982; Fent, 1986), UV polarization detectors act as a "sky compass" during navigation. Ultraviolet polarization detectors have been identified in the AM eyes of lycosid spiders (Magni et al., 1964, 1965) and the secondary eyes of certain gnaphosid and lamponid spiders (Dacke et al., 1999), but there have been no behavioral studies to determine whether salticids detect UV light polarization or use such a sky compass.

Layer III is located directly behind the central region of layer IV and is confined to a roughly circular patch in the middle of the retina (figure 1.12; plate 3) (M. F. Land, 1969a). The functions of this layer are least well understood.

In *Portia*, layer III is populated with large, irregularly arranged receptors. Unlike the secondary eye retinae, receptors in the AM eye retina are not separated by pigment. This means that the functional independence of neighboring receptors depends on them not touching. However, in layer III, rhabdoms are often contiguous, which suggests a very low spatial acuity. In some other salticids, layer III is somewhat more organized than in *Portia*, but still not to an extent that can support more than modest spatial acuity (Eakin and Brandenburger, 1971).

In most salticids, the receptor mosaic of layer II has rhabdoms that are more regularly arranged and in which the rhabdomeres are less erratically contiguous than in layer III. However, this is not the case in *Portia*. *Portia*'s layer II is only slightly more organized than layer III (figure 1.13; plate 4). The rhabdoms in layers II and III differ in appearance, depending on whether they are derived from the outer (2a and 3a) or from the inner (2b and 3b) side, but the functional significance of how they differ is not known.

In transverse section, layers I and II have a laterally compressed strip of receptors with a slight bend in the middle. The result is a boomerang-shaped (figures 1.13

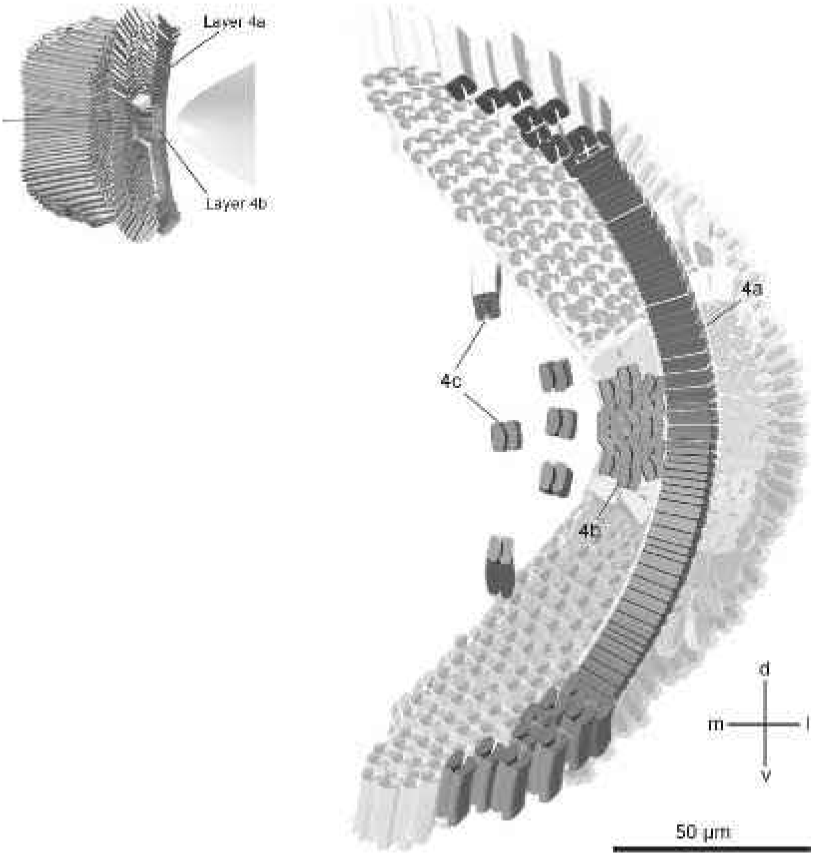

Figure 1.11
The retina of *Portia fimbriata*'s principal eye showing layer IV (shown in blue) in detail. The position of layer IV relative to other layers within the retina is shown at the top left (view angle as in figure 1.6). The transverse profile of the retina is on the right. Three types of receptors make up layer IV. Type 4a receptors form a well-organized vertical strip that may act as a simple line detector and/or be used to analyze UV polarization. Type 4b receptors form a poorly organized central patch. Type 4c receptors are scattered to the side (their positions within the figure are approximate). No function has been hypothesized for type 4b and 4c receptors. Orientation: m, medial; l, lateral; d, dorsal; v, ventral. (See plate 2 for color version.)

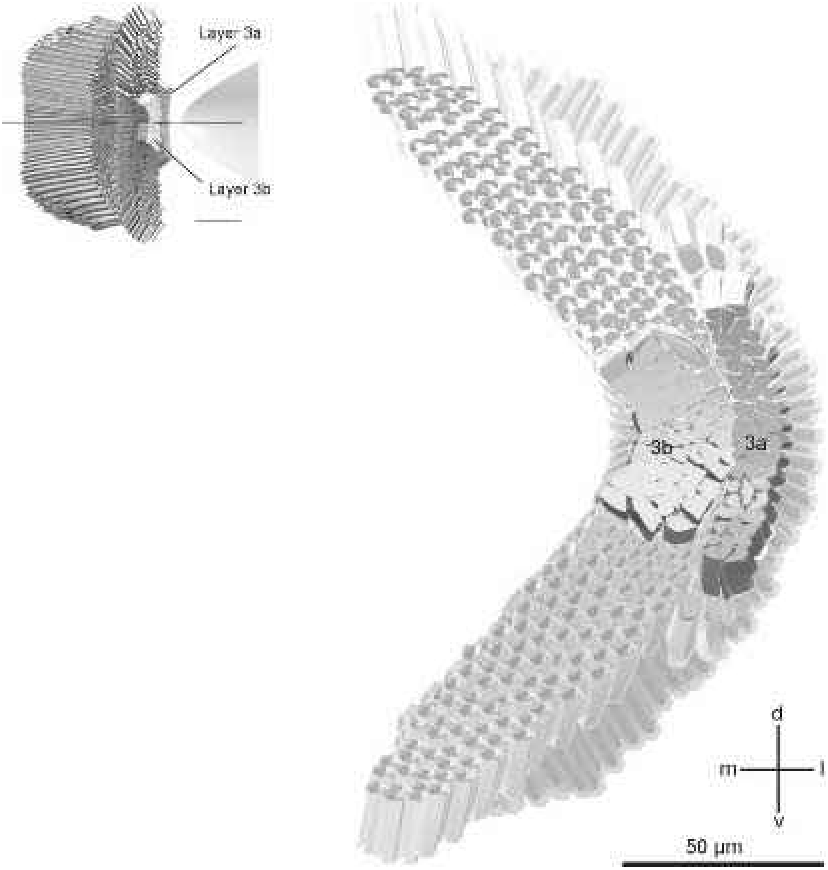

Figure 1.12
The retina of *Portia fimbriata*'s principal eye showing layer III (shown in yellow-orange) in detail. The position of layer III relative to other retinal layers is shown at the top left (view angle as figure 1.6). The transverse profile of the retina is on the right. Two types of receptors make up layer III: 3a and 3b receptors, which are large, short, irregularly disposed, and have rhabdomeres that are erratically contiguous. Layer III could receive an in-focus image in blue. The quality of any image sampled by this layer would be poor. (See plate 3 for color version.)

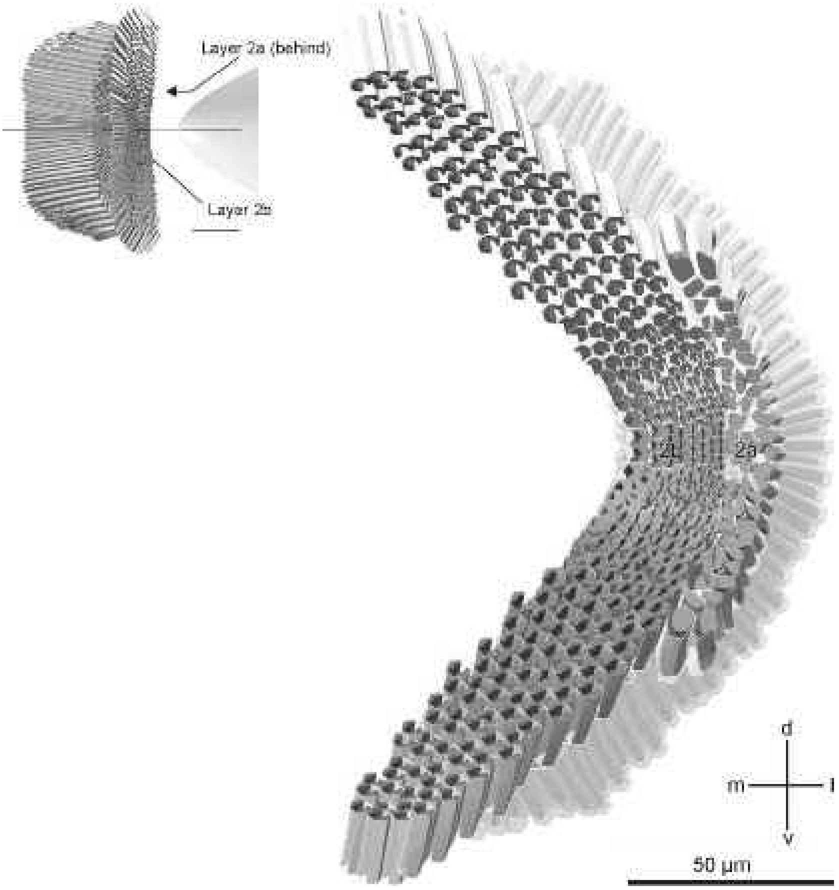

Figure 1.13
The retina of *Portia fimbriata*'s principal eye showing layer II (shown in green) in detail. The position of layer II relative to layer I is shown at the top left (view angle as in figure 1.6). The transverse profile of the retina is on the right. Two types of receptors make up boomerang-shaped layer II. At the fovea of 2b, the receptors have small interreceptor angles (although not as small as in layer I), but are arranged in a disorderly manner. The receptors increase in width toward the periphery of the boomerang arms, and the mosaic becomes more regular. Compared with layer I, the receptors in layer II are short. In *P. fimbriata*, layer II does not appear to be adapted for high-acuity vision. Orientation: d, dorsal; v, ventral; m, median; l, lateral. (See plate 4 for color version.)

and 1.14; plates 4 and 5) receptor mosaic in each of these layers, the boomerang of layer II lying over that of layer I. In *Portia*, receptor width, and therefore interreceptor spacing, in the central region of layer II (i.e., the region close to the optical axis), tends to be much greater than in the central region of layer I. This means that the central region of layer II has much lower spatial acuity. In layers I and II, receptor width and spacing tend to increase steadily toward the periphery until, at the ends of the boomerang's arms, interreceptor spacing for layers I and II roughly matches (figures 1.13 and 1.14).

Compared with the relatively high acuity of their central regions, the peripheral regions of layers I and II support only low spatial acuity. The structure of the secondary lens appears to be responsible for image quality rapidly falling off away from the fovea (Blest and Price, 1984). Close to the optical axis, the secondary lens magnifies without distortion, but the steep sides of the pit produce a distorted image away from the optical axis.

Because of its low acuity, the function of the peripheral retina probably differs from that of the central retina. For example, the periphery of layers II and I may play a role in stimulating eye tube movements (see later discussion) that line up the center of the retina on moving stimuli (Blest and Price, 1984).

The receptors in both layers II and I have almost identical absorbency spectra (figure 1.10B) (Blest et al., 1981). It is unlikely that layer II plays a role in shape perception because its image is out of focus whenever the layer I image is in focus. Perhaps layer II functions in detecting light intensity (Blest et al., 1981), has a role in pattern recognition that somehow complements the role of layer I (Blest and Price, 1984), or works with the secondary eyes to center the AM retinas on moving objects.

High-Acuity Vision: Layer I

Only layer I has the fine, regular mosaic of receptors necessary for detailed vision (figure 1.14). The internal structure of the receptors, their width and length, and their spacing in relation to other receptors are all factors that when combined define sampling performance. In the foveal region of layer I, the rhabdomeres are narrow and densely packed, which maximizes spatial sampling. In the fovea, neighboring receptors have a center-to-center spacing as low as 1.4 μm, which appears to be optimal. The rhabdomeres in layer I are also separated by cytoplasm-filled spaces, which helps isolate them optically.

Compared with other layers, layer I receptors are long, with the longest and narrowest in the fovea (figure 1.9). The additional length improves the probability that photons entering the comparatively narrow receptor will be absorbed (and hence detected).

The receptors in layer I also appear to function as light guides, which improves sampling quality in two ways. First, only light in focus on the receptor's distal tip is accepted; this reduces the probability that photons will be lost to a neighboring

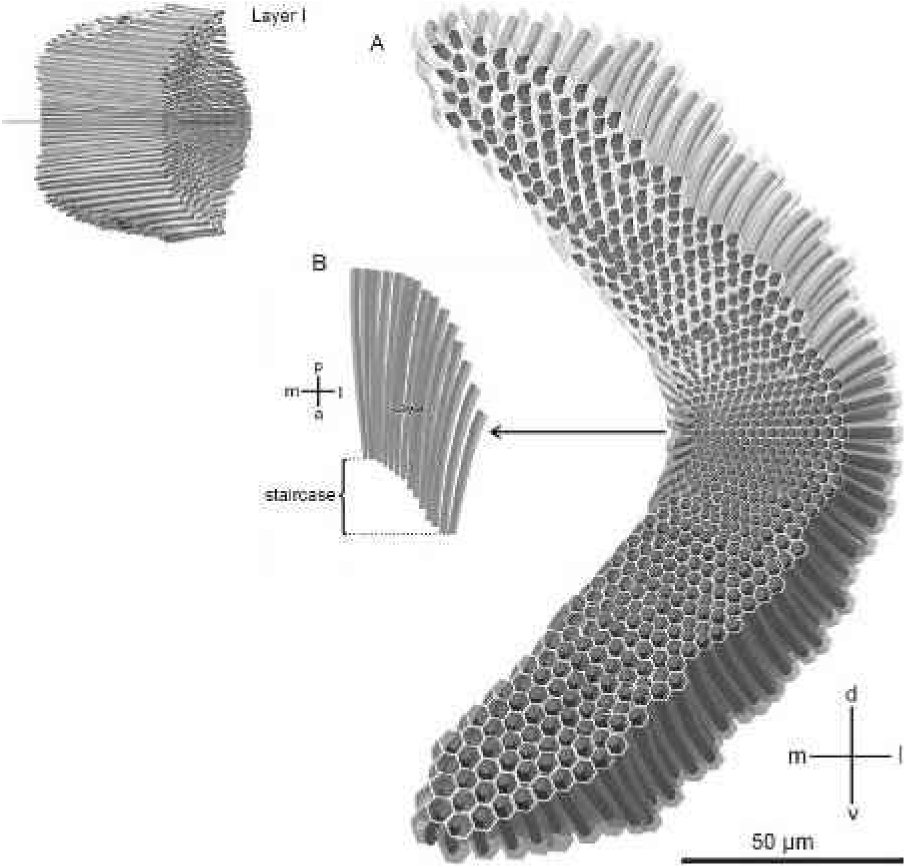

Figure 1.14
The retina of *Portia fimbriata*'s principal eye showing layer I (shown in red). The top left shows a view 55 deg to the medial side of the optical axis (view angle as in figure 1.6). (*A*) Transverse profile of the retina showing the detail of the layer's boomerang-shaped mosaic. Layer I receptors are characteristically long, with a hexagonal cross-section. The mosaic is regular, formed by rows of receptors. Receptive segments (rhabdomeres) tend to be well separated (reducing interreceptor interference), with spacing as little as 1.4 µm at the fovea. There is a gradual increase in receptor size (and spacing), and a gradual decrease in receptor length toward the periphery of the boomerang arms. (*B*) Longitudinal view from above of a row of foveal receptors. These receptors are longest and arranged like a staircase. Images of objects located from a few body lengths distant out to infinity come into focus on the distal (anterior) tips of one or more receptors. Orientation: d, dorsal; v, ventral; m, median; l, lateral. (See plate 5 for color version.)

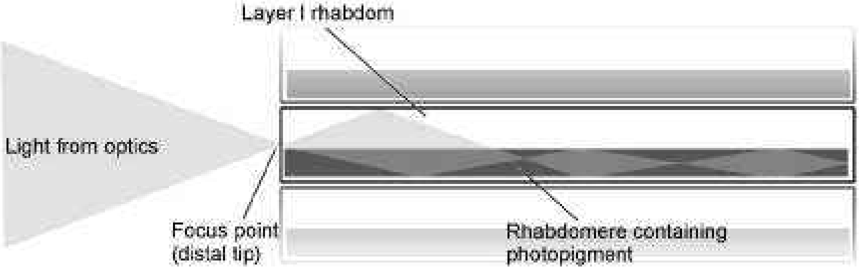

Figure 1.15
Layer I receptor acting as a light guide. Light focused on the rhabdom's anterior tip is trapped in the rhabdomere by internal reflection. Light passes back and forth through rhodopsin in the rhabdomere, enhancing its probability of being absorbed (detected).

receptor. Second, the receptors act as fiber optic cables. This effect is a consequence of the interior of the rhabdomeres being more dense than the surrounding cytoplasm. Photons entering a rhabdomere tend to get trapped by reflecting off of the optically dense rhabdomere edges. Total internal reflection enhances the likelihood that a photon will be absorbed (figure 1.15).

Layer I is specialized for resolving fine-grain spatial details, but sampling ability also depends on image quality. As noted, layers other than I have large receptors and poor sampling quality. In fact, the poor sampling quality of the more distal layers, II–IV, may be necessary for layer I to receive a maximally detailed image (D. C. Williams and McIntyre, 1980; Blest et al., 1981); that is, the interreceptor spacing and the way in which the receptors are arranged in layers II–IV diminish these layers' spatial acuity, but only minimally degrade the image received by layer I.

The minimum interreceptor angle in *Portia*'s layer I fovea is 0.04 deg (2.4 arc min) (Williams and McIntyre, 1980). In practical terms, this means that, from a distance of 200 mm, *Portia* should be able to discriminate between objects spaced 0.12 mm apart.

Compensating for Fixed-Focus Optics

The narrow receptors in the salticid's fovea can work as light guides only as long as light is focused on their distal tips. Unlike a vertebrate's eye, the salticid AM eye is a fixed lens system; i.e., it cannot accommodate. Hence, objects at different distances will come into focus at different distances behind the AM lens. For any specific receptor in layer I, when a close object is in focus on the receptor's distal tip, more distant objects tend to be out of focus (and vice versa). However, having the receptors arranged in a spatial pattern that eliminates the need for accommodation solves this potential problem.

Different parts of the foveal region of layer I are positioned on a "staircase" so that their distal tips are at different distances behind the lens (figure 1.14B). Hence, images of objects at different distances come into focus on different "stairs." The depth of the staircase (~20 µm) is sufficiently large to allow an in-focus image to form on at least one of the "stairs" from approximately two body lengths away to infinity (Blest et al., 1981). Only the layer I fovea has this structure.

The Active Principal Eye

Telephoto optics in conjunction with the unique structure of the AM retina appears to provide a solution to the problem of how a fixed-lens eye can provide both color discrimination and high spatial resolution. However, as a tradeoff, there is a drastic reduction in the AM retina's field of view. *Portia*'s layer I fovea is only fifteen receptors across, giving it a field of view little more than 0.6 deg wide, much less than the ~30–40 deg provided by the corneal lenses. What is more, most objects examined by the eye will be out of focus at some part of the "staircase," making the fovea's effective field of view even narrower. Despite these limitations, the fovea supports the remarkable feats of visual discrimination that underlie much of *Portia*'s complex, flexible behavior.

The AM eye is an "active" eye and this may be the key to understanding how the AM retina's narrow field of view works. Movement of the eye's field of view over a scene probably forms a critical part of how perception works for salticids (Kaps and Schmid, 1996). Using six muscles attached to its outside, each AM eye tube can be moved with three degrees of freedom: vertical, horizontal, and rotational (figure 1.16) (M. F. Land, 1969b). These are the same three degrees of freedom with which our own eyes move, although we are typically unconscious of the small rotational movements (McIlwain, 1996).

Small lateral eye-tube movements allow the salticid to sweep the layer I "staircase" over an object in the visual field, and larger eye movements allow this spider to sample the larger image projected by the corneal lens. The movements of the AM eyes, which can be complex, are probably a critical factor in how salticids process visual information, especially shape and form (M. F. Land, 1969b; M. F. Land and Furneaux, 1997).

Each boomerang-shaped AM retina sits in the salticid's cephalothorax with its "elbow" pointing out laterally (see figure 1.14). However the optics of the eyes invert the image both vertically and horizontally. The resulting fields of view of the two AM retinas, when held together, form an "X," with the fields of view of the two foveas not quite intersecting (see figures 1.6 and 1.17).

The X can be moved in four basic ways. The first is with wide-angle spontaneous scanning movements (figure 1.17A). At varying speeds, the center of the AM retina wanders over a large horizontal and vertical field, possibly searching for objects on which to fixate. These movements may cover the entire visual field of the AM eyes. The second is with saccades (figure 1.17B). These are rapid movements in which the centers of the retinas of both AM eyes move to fixate on some object that has just moved. Third is tracking (figure 1.17C). These are movements that keep the retinae

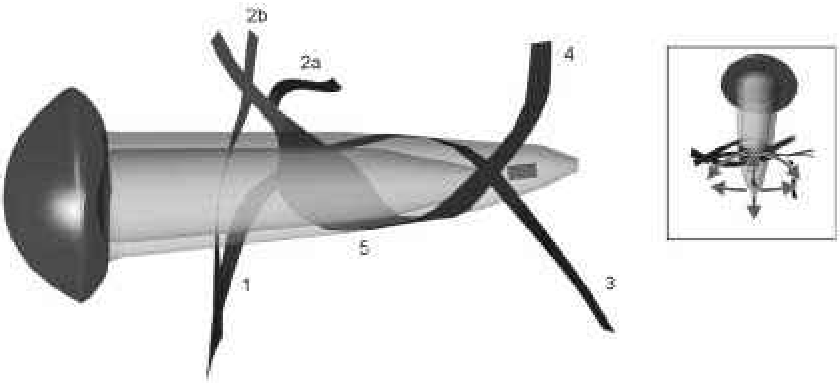

Figure 1.16
Top view of *Portia fimbriata*'s left AM eye showing probable positions of eye muscles. Five muscle bands attached to the eye tube allow the retina to be moved (inset) in the horizontal and vertical planes, and rotated about 30 deg in either direction. Although the corneal lens is wider than the eye tube (giving the eye its distinctive "mushroom" shape), the retina's field of view is never blocked because at any one time it samples only a small part of the corneal lens's field of view and because it can be moved to where the images from the sides of the corneal lens are visible. (The muscles and their numbers are taken from M. F. Land, 1969b. The eye tube is adapted from D. S. Williams and McIntyre, 1980.)

of both AM eyes fixated on a moving object. The fourth is scanning (figure 1.17D). Scanning occurs after the AM retinae fixate on a new target. During scanning, the most complex of the four movement patterns, the AM retinae move back and forth across an object at 0.5–1 Hz (approximately over the width of the layer I "staircase"), while they slowly rotate through an arc of about 50 deg.

In spite of their potential heuristic value, there are as yet no detailed studies of the movements of *Portia*'s AM eyes. However, it is known that the AM eyes of *Portia fimbriata* are more active than those of any other species that has been examined (D. S. Williams and McIntyre, 1980). In fact, they move almost continuously, even in complete darkness (D. P. Harland, unpublished results).

What the AM Eye Sees

The small window of high spatial acuity provided by layer I in the AM eye may have important implications for the kinds of fine-grained optical cues potentially available to *Portia*. Behavioral investigations of the optical cues that *Portia fimbriata* uses to discriminate between prey and nonprey has confirmed what the structural and optical investigation of the principal eye suggests. A number of critical visual cues are provided by very small, specific regions of the prey's body (Harland and Jackson, 2000a). The limited field of view provided by the AM retina means that when one region of the prey is under inspection, other regions are no longer in clear view. The

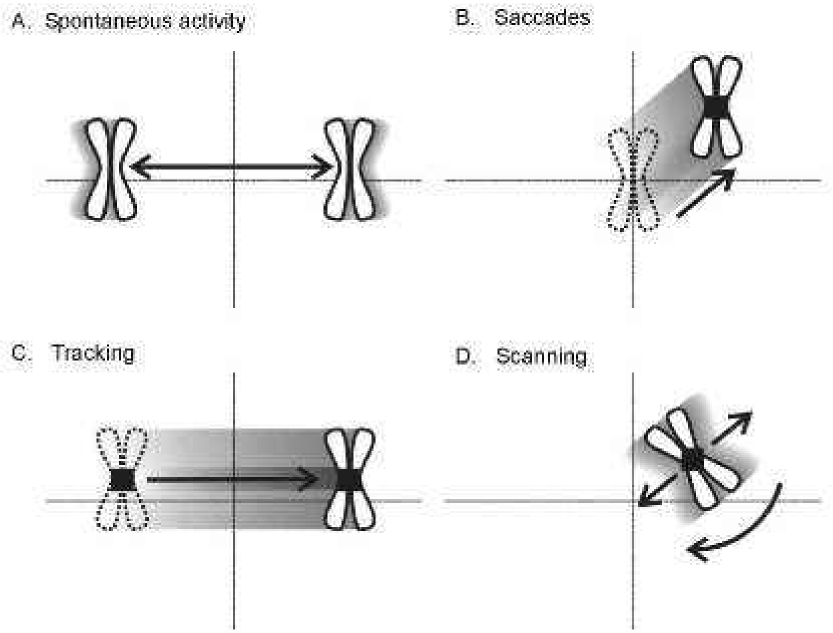

Figure 1.17
Summary of four types of eye movement made by the salticid anterior median eye. Fields of view from two boomerang-shaped retinae combine to create an X-shaped field of view. The arrows indicate retinal movement. (*A*) Spontaneous activity; retinae move unpredictably over a scene. (*B*) Saccades; fields of view are fixated on an object (the black square). (*C*) Tracking; keeps retinae fixed on a moving object. (*D*) Scanning; a newly acquired object is examined by moving fields of view back and forth while slowly rotating one way, then another. (Adapted from M. F. Land, 1969b.)

way in which the visual world is structured from such small high-resolution images appears to depend on both the pattern of the spider's eye movements and its ability to remember what cues it has seen.

Portia's Umwelt

Although salticids rely on more than one sensory modality, vision is primary. Unlike any other spider, a salticid locates, tracks, stalks, chases down, and leaps on active prey, with all phases of the predatory sequence under visual control (Forster, 1982a). Using visual cues alone, salticids discriminate between mates and rivals, predators and prey, and different types of prey, as well as other features of their environment (Crane, 1949; Drees, 1952; Heil, 1936; Jackson and Pollard, 1996; Tarsitano and Jackson, 1997; Harland et al., 1999; Harland and Jackson 2000a, 2001, 2002).

Much of human behavior, and cognition, is vision based (Dennett, 1991). Hence, we may overestimate the advantages of vision and underestimate what can be done with other sensory modalities. This potential bias notwithstanding, it seems to be the case that *Portia's* acute eyesight has a profound influence on both its behavior and its putative cognitive abilities. *Portia*'s detouring behavior illustrates this point especially clearly.

Portia's ability to plan and execute long detours requires visual acuity sufficient to examine the spatial relations between objects from a distance (Tarsitano and Andrew, 1999). This visual acuity also enables it to accurately identify the location and behavior of its prey from a distance (Jackson, 1995; D. Li and Jackson, 1996; D. Li et al., 1997). All of this visual information is critical in enabling *Portia* to execute its flexible predatory tactics.

Almost a century ago, Jakob von Uexküll (1909) considered how sensory systems, styles of behavior, and cognitive profiles are interrelated. No animal, including humans, has simple, direct access to an independent physical universe. Instead, each operates inside a subjective "model" of the world (von Uexküll, 1934), or what von Uexküll (1909) called the animal's *Umwelt*. This is roughly translated as an animal's "self-world" (C. Schiller, 1957), a product of the organism's sensory intake, internal state, central processing capabilities, and motor patterns.

Natural selection sees to it that the *Umwelt* is not arbitrary (e.g., Dawkins, 1996); it has to work for the animal, enabling it to survive and propagate. However, a critical insight of von Uexküll's is that one can expect important differences among animals in the character of how they experience what is to them the outside world (Deely, 2001).

Obtaining an understanding of *Portia*'s *Umwelt* may be a tractable problem, but it should not be confused with the notion that we might somehow come to know directly what it is like to be a *Portia* (e.g., Nagel, 1974). Although studying its sensory systems, behavior, and cognitive processes will never reveal to us precisely what it is like to be *Portia*, this is a valid approach to learning something more tangible. Although it is no trivial task, we can expect eventually to comprehend *Portia*'s *Umwelt*. Although we are still a long way from this goal, we may be able to shed light on some of the most interesting issues with a final story.

In a Queensland rain forest, we find *Portia fimbriata* sitting on a portion of a vine that has fallen away from a tree trunk (figure 1.18A; plate 6). Based on what we know about this araneophagic predator, we think that *Portia* is prepared, in a way that we are not, to perceive webs, spider-sized animals, and potential pathways to the web via the vine and neighboring vegetation.

Of course, *Portia*'s *Umwelt* is built from more than just visual information. In this story, for example, its feet and palps have touched silk lines on the vine's surface, triggering a number of chemoreceptors. Some of the silk is from *Jacksonoides queenslandicus*, and airborne chemical cues carry the odor of this spider. However, the source of information may not be important for *Portia*. In this example, chemosensory information from *J. queenslandicus* may prime *Portia* to detect visual cues associated with this familiar prey.

One way of interpreting such a priming effect is to suggest that chemical cues elicit some kind of representation of *J. queenslandicus* somewhere in *Portia*'s central nervous system, although what this representation might be is not clear. Certainly, it need not be anything like a picture of or the idea of the prey (Gardenfors, 1996). A more plausible explanation might be that the chemosensory information lowers the thresholds for responses by central nervous system modules (or feature detectors) associated with the visual system. What we do know is that chemosensory and visual information work together to underpin predatory behaviors appropriate for capturing *J. queenslandicus*. We are still a long way from understanding precisely how this is done, however.

The question of whether *Portia*'s *Umwelt* includes anything like the visual images (or "pictures") that we see remains unresolved, but the extraordinary eyesight of these spiders encourages us to explore this possibility. Acute vision may indeed be a central pillar of an *Umwelt* that requires recognizing distinct objects distributed at precise locations in space. This is, of course, what humans experience, and it may be reasonable to assume that *Portia's* experiences are similar. On the other hand, given that the structural details of *Portia*'s eyes are so different from ours, we should also expect important differences in the subjective world that they help to create.

Movement of objects in the outside world must be a highly relevant part of *Portia*'s *Umwelt*. The anterior lateral eyes provide input about movement within a range of 45 deg to either side of the spider (figure 1.18C); the remaining secondary eyes gather movement information beyond that, and even behind *Portia*'s body.

Portia's Umwelt probably includes objects positioned at more or less precise distances, and the AL eyes probably play a major role in providing that information. The AL eyes' fields of view overlap directly in front of *Portia*, and toward the center of the visual field, the visual angle between receptors decreases from approximately 1 deg to just 0.4 deg. A disparity between the images in the AL retinae probably provides information about an object's distance. Information about additional features of the visual world, such as an object's shape, size, and color, are probably provided by the anterior medial eyes.

In this final story, for example, information from the AL eyes has directed the AM eye tubes to move their tiny field across the scene provided by the AM corneal lenses (figure 1.18D). Its AM eyes are now examining a moving object that is slightly off center. As explained earlier, the AM eye tubes are highly active, and our hypothesis is that this "scanning" activity serves to abstract relevant information from the retinal images. Input from particularly salient cues may in turn trigger patterns of scanning designed to search for certain additional visual cues that the initial cues have primed the spider to recognize. Perhaps through this type of sequential scanning for particular cues, a central nervous system-based representation of the object is constructed (figure 1.18F). The salticid eye may be surprisingly good at assessing the details of objects. However, as a consequence of doing its analysis via eye-tube movements and using a retina with only a small number of receptors, it probably takes much more time than analogous processing by a vertebrate.

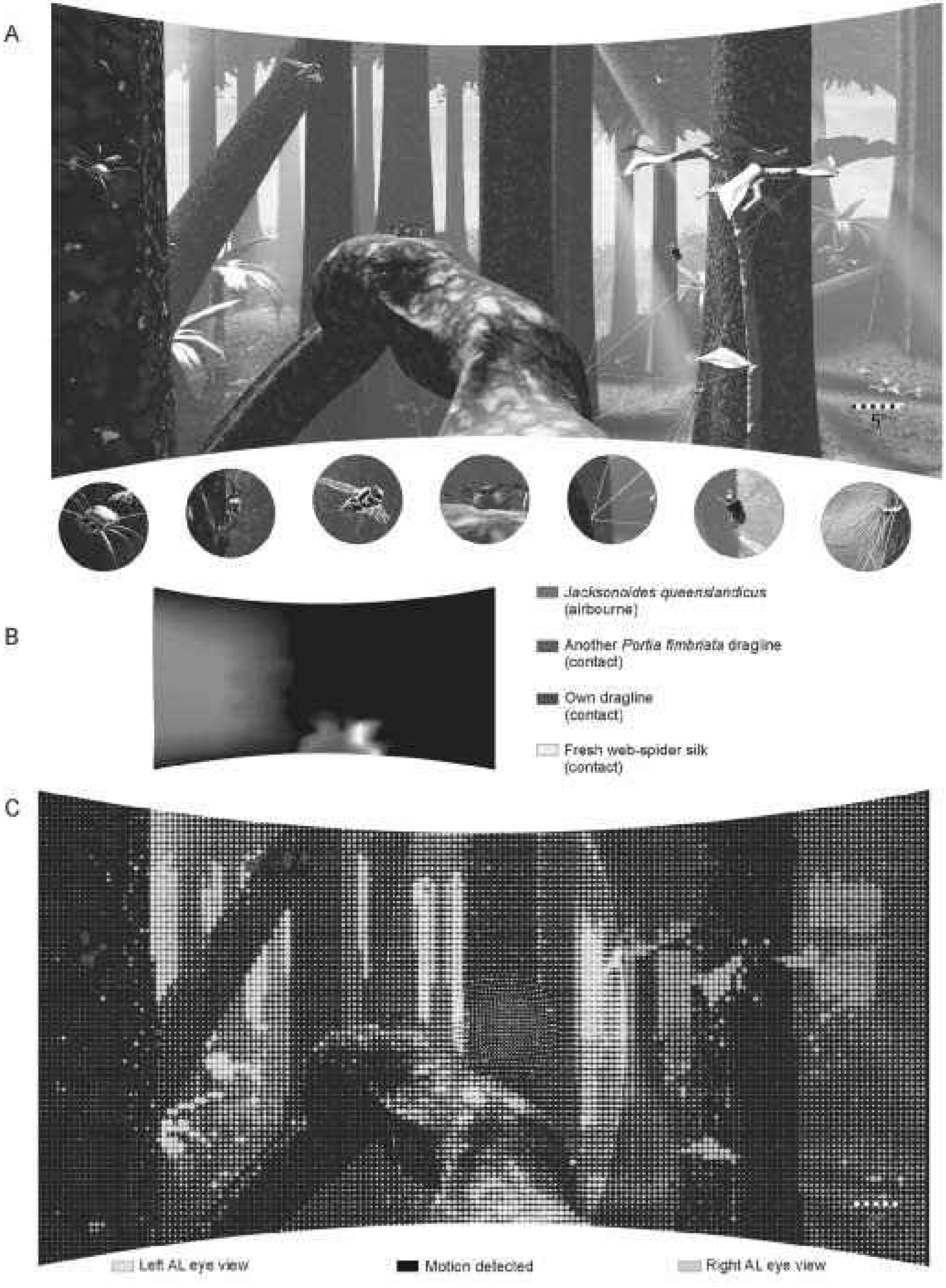

Figure 1.18
Portia fimbriata's view of the world. (*A*) *Portia*'s forest habitat (approximately 90 deg wide). The circles show some key points of interest for *Portia*. (*B*) Representation of *Portia*'s

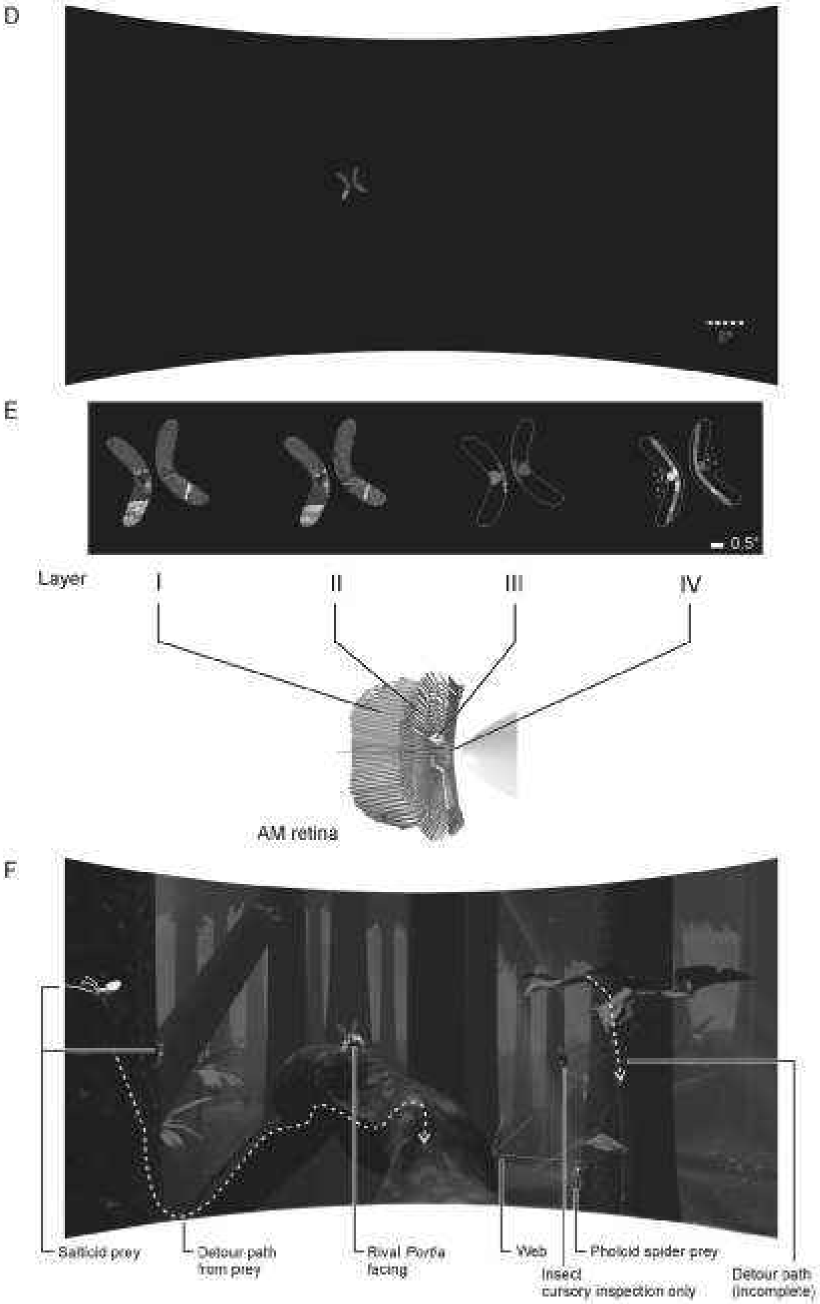

Figure 1.18 (continued)
chemoreceptive environment. (*C*) Representation of the view seen by anterior lateral eyes. Note the region of binocular overlap used in range-finding and foveal regions. (*D*) Field of view provided by anterior median eyes. (*E*) View seen by the four layers of the AM eyes during inspection of other *Portia*. (*F*) View showing elements that *Portia* has abstracted from the scene using its AM eyes during several minutes of looking around. (See plate 6 for color version.)

Watching *Portia* pursue prey tends to be a drawn-out exercise; this spider moves through its predatory sequence at a speed that is tedious for a human observer. It may be the case that a unique (or at least a nonhuman) sense of time is a key part of *Portia's Umwelt*. The slowness of scanning-based construction of an object suggests interesting ways in which the perception of time by *Portia* might differ from our own notion of time.

Although this limited attempt to characterize *Portia's Umwelt* does not put us directly in this spider's shoes, it is a necessary, initial step toward its reverse engineering (Dennett, 1995). That in turn can be a step toward building a robot that can solve problems and behave as *Portia* does. Knowing what it is like to be *Portia* may amount to much the same thing.

References

Aho, A. C., Donner, K., Hyden, C., Larsen, L. O., and Reuter, T. (1988) Low retinal noise in animals with low body-temperature allows high visual sensitivity. *Nature* 334: 348–350.

Ahyong, S. T. and Harling, C. (2000) The phylogeny of the stomatopod Crustacea. *Aust. J. Zool.* 48: 607–642.

Alloway, T. M. (1972) Learning and memory in insects. *Ann. Rev. Entom.* 17: 43–56.

Altman, J. S. and Kien, J. (1986) A model for decision making in the insect nervous system. In M. A. Ali (ed.), *Nervous Systems in Invertebrates*. New York: Plenum, pp. 621–643.

Ameyaw-Akumfi, C. and Hazlett, B. A. (1975) Sex recognition in the crayfish *Procambarus clarkii*. *Science* 190: 1225–1226.

Anderson, C. W. (1993) Modulation of feeding behavior in response to prey type in the frog *Rana pipiens*. *J. Exp. Biol.* 179: 1–11.

Anderson, C. W. and Nishikawa, K. C. (1993) A prey-type dependent hypoglossal feedback system in the frog, *Rana pipiens*. *Brain Behav. Evol.* 42: 189–196.

Anderson, C. W. and Nishikawa, K. C. (1996) The roles of visual and proprioceptive information during motor program choice in frogs. *J. Comp. Physiol. A* 179: 753–762.

Anderson, C. W. and Nishikawa, K. C. (1997a) Sensory modulation and behavioral choice during feeding in the Australian frog, *Cyclorana novaehollandiae*. *J. Comp. Physiol. A* 180: 187–202.

Anderson, C. W. and Nishikawa, K. C. (1997b) The functional anatomy and evolution of hypoglossal afferents in the leopard frog, *Rana pipiens*. *Brain Res.* 771: 285–291.

Antal, M., Matsumoto, N., and Székely, G. (1986) Tectal neurons of the frog: Intracellular recording and labeling with cobalt electrodes. *J. Comp. Neurol.* 246: 238–253.

Arbib, M. A. (1987) Advantages of experimentation in neuroscience. *Behav. Brain Sci.* 10: 368–369.

Arbib, M. A. (1989) Visuomotor coordination: Neural models and perceptual robotics. In J.-P. Ewert and M. A. Arbib (eds.), *Visuomotor Coordination: Amphibians, Comparisons, Models and Robots*. New York: Plenum, pp. 121–171.

Arikawa, K. (1999) Color vision. In E. Eguchi and Y. Tominaga (eds.), *Atlas of Sensory Receptors of Arthropods—Dynamic Morphology in Relation to Function*. Tokyo: Springer-Verlag, pp. 23–32.

Arikawa, K. and Stavenga, D. G. (1997) Random array of colour filters in the eyes of butterflies. *J. Exp. Biol.* 200: 2501–2506.

Arikawa, K. and Kinoshita, M. (2000) Learning by microbrain—From the study of color vision in Papilio. In T. Kato (ed.), *Frontiers of the Mechanisms of Memory and Dementia*. Amsterdam: Elsevier, pp. 3–6.

Arikawa, K. and Uchiyama, H. (1996) Red receptors dominate the proximal tier of the retina in the butterfly *Papilio xuthus*. *J. Comp. Physiol. A* 178: 55–61.

Arikawa, K., Inokuma, K., and Eguchi, E. (1987) Pentachromatic visual system in a butterfly. *Naturwissenschaften* 74: 297–298.

Arikawa, K., Mizuno, S., Scholten, D. G. W., Kinoshita, M., Seki, T., Kitamoto, J., and Stavenga, D. G. (1999a) An ultraviolet absorbing pigment causes a narrow-band violet receptor and a single-peaked green receptor in the eye of the butterfly *Papilio*. *Vision Res.* 39: 1–8.

Arikawa, K., Scholten, D. G. W., Kinoshita, M., and Stavenga, D. G. (1999b) Tuning of photoreceptor spectral sensitivities by red and yellow pigments in the butterfly *Papilio xuthus*. *Zool. Sci.* 16: 17–24.

Aronson, R. B. (1991) Ecology, paleobiology and evolutionary constraint in the octopus. *Bull. Mar. Sci.* 49: 245–255.

Atema, J. (1985) Chemoreceptors in the sea: Adaptations of chemoreceptors and behaviour to aquatic stimulus conditions. *Symp. Soc. Exp. Biol.* 39: 387–423.

Autrum, H. (1950) Die Belichtungspotentiale und das Sehen der Insekten (Untersuchungen an *Calliphora* und *Dixippus*). *Z. Vergl. Physiol.* 32: 176–227.

Autrum, H. and Stöcker, M. (1952) Über optische Verschmelzungsfrequenzen und stroboskopisches Sehen bei Insekten. *Biol. Zentr.* 71: 129–152.

Autrum, H. and von Zwehl, V. (1964) Die spektrale Empfindlichkeit einzelner Sehzellen des Bienenauges. *Z. Vergl. Physiol.* 48: 357–384.

Baba, Y. and Shimozawa, T. (1997) Diversity of motor responses initiated by a wind stimulus in the freely moving cricket, *Gryllus bimaculatus*. *Zool. Sci.* 14: 587–594.

Backhaus, W. (1991) Color opponent coding in the visual system of the honeybee. *Vison Res.* 31: 1381–1397.

Backhaus, W. (1992a) Colour vision in honeybees. *Neurosci. Biobehav. Rev.* 16: 1–12.

Backhaus, W. (1992b) The Bezold-Brücke effect in the color vision system of the honeybee. *Vision Res.* 32: 1425–1431.

Backhaus, W. and Menzel, R. (1987) Color distance derived from a receptor model of color vision in the honeybee. *Biol. Cybern.* 55: 321–331.

Bacon, J. P. (1980) An homologous interneurone in a locust, a cricket and a mantid. *Verh. Dtsch. Zool. Ges.* 73: 300.

Bacon, J. P. and Murphey, R. K. (1984) Receptive fields of cricket (*Acheta domesticus*) interneurones are related to their dendritic structure. *J. Physiol. Lond.* 352: 601–623.

Baddeley, A. (1993) *Your Memory: A User's Guide*. London: Penguin.

Baerends, G. P. (1987) Ethology and physiology: A happy marriage. *Behav. Brain Sci.* 10: 369–370.

Bandai, K., Arikawa, K., and Eguchi, E. (1992) Localization of spectral receptors in the ommatidium of butterfly compound eye determined by polarization sensitivity. *J. Comp. Physiol. A* 171: 289–297.

Banschbach, V. S. (1994) Colour association influences honey bee choice between sucrose concentrations. *J. Comp. Physiol. A* 175: 107–114.

Bardach, J. E. and Villars, T. (1974) The chemical senses of fishes. In P. T. Grant and A. M. Mackie (eds.), *Chemoreception in Marine Organisms*. London: Academic Press, pp. 49–104.

Barlow, H. B. (1953) Summation and inhibition in the frog's retina. *J. Physiol. Lond.* 119: 69–88.

Barlow, H. B. (1982) What causes trichromacy? A theoretical analysis using comb-filtered spectra. *Vison Res.* 22: 635–643.

Barnes, R. D. (1987) *Invertebrate Zoology*, 5th ed. Philadelphia, Pa.: Saunders.

Barth, F. G. (1985) Slit sensilla and the measurement of cuticular strains. In F. G. Barth (ed.), *Neurobiology of Arachnids*. Berlin: Springer-Verlag, pp. 162–188.

Barth, F. G., Wastl, U., Humphrey, J. A. C., and Devarakonda, R. (1993) Dynamics of arthropod filiform hairs. II. Mechanical properties of spider trichobothria (*Cupiennius salei* Keys.). *Phil. Trans. Roy. Soc. Lond. B* 340: 445–461.

Bartley, J. A. (1983) Prey selection and capture by the Chinese mantid (*Tenodera sinensis*, Saussure). Ph.D. dissertation, Univ. of Delaware, Newark, Delaware.

Baumann, F., Mauro, A., Milecchia, R., Nightingale, S., and Young, J. Z. (1970) The extraocular light receptors of the squids *Todarodes* and *Illex*. *Brain Res.* 21: 275–279.

Bekoff, M. (2000) Animal emotions: Exploring passionate natures. *Bioscience* 50: 861–870.

Belisle, C. and Cresswell, J. (1997) The effects of limited memory capacity on foraging behavior. *Theoret. Pop. Biol.* 52: 78–90.

Bennett, A. T. and Cuthill, I. C. (1994) Ultraviolet vision in birds: What is its function? *Vison Res.* 34: 1471–1478.

Berger, F. A. (1985) Morphologie und physiologie einiger visueller interneuronen in den optischen ganglien der gottesanbeterin *Mantis religiosa*. Doctoral dissertation, University of Düsseldorf, Düsseldorf, Germany.

Bernard, G. D. (1979) Red-absorbing visual pigment of butterflies. *Science* 203: 1125–1127.

Bernard, G. D. and Miller, W. H. (1970) What does antenna engineering have to do with insect eyes? *IEEE Stud. J.* 8: 2–8.

Bernard, G. D. and Remington, C. L. (1991) Color vision in Lycaena butterflies: Spectral tuning of receptor arrays in relation to behavioral ecology. *Proc. Natl. Acad. Sci. U.S.A.* 88: 2783–2787.

Bernard, G. D. and Wehner, R. (1977) Functional similarities between polarization vision and color vision. *Vison Res.* 17: 1019–1028.

Bernard, G. D., Douglas, J., and Goldsmith, T. H. (1988) Far-red sensitive visual pigment of a metalmark butterfly. *Invest. Ophthalmol. Suppl.* 29: 350.

Bernhards, H. (1916) Der bau des komplexauges von astacus fluviatilis (*Potamobius astacus* L.). Ein beitrag zur morphologie der decapoden. *Z. Wiss. Zool.* 114: 649–707.

Besharse, J. C. and Iuvone, P. M. (1992) Is dopamine a light-adaptive or a dark-adaptive modulator in retina? *Science* 216: 1250–1252.

Bieger, D. and Neuman, R. S. (1984) Selective accumulation of hydroxytryptamines by frogs' tectal neurons. *Neuroscience* 12: 1167–1177.

Binns, E. E. (1999) The synaptic pharmacology underlying sensory processing in the superior colliculus. *Neurobiology* 59: 129–159.

Bitterman, M. E. (1986) Vertebrate-invertebrate comparisons. In H. J. Jerison and I. Jerison (eds.), *Intelligence and Evolutionary Biology*. NATO Advanced Study Institute on Evolutionary Biology of Intelligence (Popi, Italy), Berlin: Springer-Verlag, pp. 251–276.

Blest, A. D. (1983) Ultrastructure of secondary retinae of primitive and advanced jumping spiders (Araneae, Salticidae). *Zoomorphology* 102: 125–41.

Blest, A. D. (1985a) The fine structure of spider photoreceptors in relation to function. In F. G. Barth (ed.), *Neurobiology of Arachnids*. Berlin: Springer-Verlag, pp. 79–102.

Blest, A. D. (1985b) Retinal mosaics of the principal eyes of jumping spiders (Salticidae) in some neotropical habitats: Optical trade-offs between sizes and habitat illuminances. *J. Comp. Physiol. A* 157: 391–404.

Blest, A. D. (1987a) Comparative aspects of the retinal mosaics of jumping spiders. In A. P. Gupta (ed.), *Arthropod Brain: Its Evolution, Development, Structure and Function*. New York: Wiley, pp. 203–229.

Blest, A. D. (1987b) The retinae of *Euryattus bleekeri*, an aberrant salticid spider from Queensland. *J. Zool. Lond.* 211: 399–408.

Blest, A. D. and Land, M. F. (1977) The physiological optics of *Dinopis subrufus* L. Koch: A fish-lens in a spider. *Proc. Roy. Soc. Lond. B* 196: 197–222.

Blest, A. D. and Price, G. D. (1984) Retinal mosaics of the principal eyes of some jumping spiders (Salticidae: Araneae): Adaptations for high visual acuity. *Protoplasma* 120: 72–84.

Blest, A. D., Hardie, R. C., McIntyre, P., and Williams, D. S. (1981) The spectral sensitivities of identified receptors and the function of retinal tiering in the principal eyes of jumping spiders. *J. Comp. Physiol.* 145: 227–239.

Boal, J. G. and Golden, D. K. (1999) Distance chemoreception in the common cuttlefish, *Sepia officinalis* (Mollusca, Cephalopoda). *J. Exp. Mar. Biol. Ecol.* 235: 307–317.

Bond, A. B. (1983) Visual search and selection of natural stimuli in the pigeon: The attentional threshold hypothesis. *J. Exp. Psychol. Anim. Behav. Process.* 9: 292–306.

Borchers, H.-W. and Ewert, J.-P. (1979) Correlation between behavioral and neuronal activities of toads *Bufo bufo* (L.) in response to moving configurational prey stimuli. *Behav. Processes* 4: 99–106.

Borchers, H.-W., Burghagen, H., and Ewert, J.-P. (1978) Key stimuli of prey for toads (*Bufo bufo* L.): Configuration and movement patterns. *J. Comp. Physiol.* 128: 189–192.

Bowdish, T. I. and Bultman, T. L. (1993) Visual cues used by mantids in learning aversion to aposematically colored prey. *Am. Midl. Nat.* 129: 215–222.

Bowmaker, J. K. (1980) Colour vision in birds and the role of oil droplets. *Trends Neurosci.* 199: 196–199.

Bowmaker, J. K. (1983) Trichromatic colour vision: why only three receptor channels? *Trends Neurosci.* 6: 41–43.

Boyan, G. S. (1993) Another look at insect audition: The tympanic receptors as an evolutionary specialization of the chordotonal system. *J. Insect. Physiol.* 39: 187–200.

Boyan, G. S. and Ball, E. E. (1986) Wind-sensitive interneurones in the terminal ganglion of praying mantids. *J. Comp. Physiol. A* 159: 773–789.

Boyan, G. S. and Ball, E. E. (1989) The wind-sensitive cercal receptor/giant interneurone system of the locust, *Locusta migratoria*. II. Physiology of giant interneurones. *J. Comp. Physiol. A* 165: 511–521.

Boyan, G. S., Williams, J. L. D., and Ball, E. E. (1989) The wind-sensitive cercal receptor/giant interneurone system of the locust, *Locusta migratoria*. I. Anatomy of the system. *J. Comp. Physiol. A* 165: 539–552.

Boyle, P. R. (1977) Receptor units responding to movement in the octopus mantle. *J. Exp. Biol.* 65: 1–9.

Bradley, E. A. and Young, J. Z. (1975) Comparison of visual and tactile learning in Octopus after lesions to one of the two memory systems. *J. Neurosci. Res.* 1: 185–205.

Brandao, M. L., Anseloni, V. Z., Pandossio, J. E., De Araujo, J. E., and Castilho, V. M. (1999) Neurochemical mechnisms of the defensive behavior in the dorsal midbrain. *Neurosci. Biobehav. Rev.* 23: 863–875.

Breithaupt, T., Schmitz, B., and Tautz, J. (1995) Hydrodynamic orientation of crayfish (*Procambaraus clarkii*) to swimming fish prey. *J. Comp. Physiol. A* 177: 481–491.

Bridges, C. D. B. (1972) The rhodopsin-porphyropsin visual system. In H. J. A. Dartnall (ed.), *Handbook of Sensory Physiology*. vol. VII/I, *The Photochemistry of Vision*. Berlin: Springer-Verlag, pp. 417–480.

Brines, M. L. and Gould, J. L. (1982) Skylight polarization patterns and animal orientation. *J. Exp. Biol.* 96: 69–91.

Briscoe, A. D. (2000) Six opsins from the butterfly *Papilio glaucus*: Molecular phylogenetic evidence for paralogous origins of red-sensitive visual pigments in insects. *J. Mol. Evol.* 51: 110–121.

Briscoe, A. D. and Chittka, L. (2001) The evolution of color vision in insects. *Ann. Rev. Entomol.* 46: 471–510.

Briscoe, A. D., Bernard, G. D., Szeto, A. S., Nagy, L. M., and White, R. H. (2003) Not all butterfly eyes are created equal: Rhodopsin absorption spectra, molecular identification and localization of UV-, blue- and green-sensitive rhodopsin encoding mRNA in the retina of *Vanessa cardui*. *J. Comp. Neurol.* 458: 334–349.

Bristowe, W. S. (1958) *The World of Spiders*. London: Collins.

Brodie, E. D. (1977) Hedgehogs use toad venom in their own defense. *Nature* 268: 627–628.

Brooke, R. K., Jr. (1975) A single-lens multiband camera. *Opt. Eng.* 14: 347–350.

Brower, J. V. Z. and Brower, L. P. (1962) Experimental studies of mimicry. 6: the reaction of toads (*Bufo terrestris*) to honey bees (*Apis mellifera*) and their dronefly mimics (*Eristalis vinetorum*). *Am. Naturalist* 96: 297–307.

Browman, H. I. and Hawryshyn, C. W. (2001) Biology of ultraviolet and polarization vision. *J. Exp. Biol.* 204: 2383–2596.

Brown, T. J. and Handford, P. (2000) Sound design for vocalizations: Quality in the woods, consistency in the fields. *The Condor* 102: 81–92.

Brown, W. T. and Marker, W. B. (1977) Unit responses in the frog's caudal thalamus. *Brain Behav. Evol.* 14: 274–297.

Bruce, L. L. and Neary, T. J. (1995) The limbic system of tetrapods: A comparative analysis of cortical and amygdalar populations. *Brain Behav. Evol.* 46: 224–234.

Bryceson, K. P. (1986) Short Communication. The effect of screening pigment migration on spectral sensitivity in a crayfish reflecting superposition eye. *J. Exp. Biol.* 125: 401–404.

Brzoska, J. and Schneider, H. (1978) Modification of prey-catching behavior by learning in the common toad (*Bufo b. bufo* L., Anura, Amphibia): Changes in response to visual objects and effects of auditory stimuli. *Behav. Processes* 3: 125–136.

Buchner, E. (1984) Behavioral analysis of spatial vision in insects. In M. A. Ali (ed.), *Photoreception and Vision in Invertebrates*. New York: Plenum, pp. 561–621.

Budelmann, B. U. (1994) Cephalopod sense organs, nerves and the brain: Adaptations for high performance and life style. *Mar. Freshwater Behav. Physiol.* 25: 13–33.

Budelmann, B. U. (1996) Active marine predators: The sensory world of cephalopods. *Mar. Freshwater Behav. Physiol.* 27: 59–75.

Budelmann, B. U. and Bleckmann, H. (1988) A lateral line analogue in cephalopods: Water waves generate microphonic potentials in the epidermal head lines of *Sepia* and *Lolliguncula*. *J. Comp. Physiol.* A 164: 1–5.

Budelmann, B. U. and Williamson, R. (1994) Directional sensitivity of hair cell afferents in the Octopus statocyst. *J. Exp. Biol.* 187: 245–259.

Budelmann, B. U. and Young, J. Z. (1984) The statocyst-oculomotor system of *Octopus vulgaris*: Extraocular eye muscles, eye muscle nerves, statocyst nerves and oculomotor centre of the central nervous system. *Phil. Trans. Roy. Soc. Lond. B* 306: 159–189.

Budelmann, B. U. and Young, J. Z. (1993) The oculomotor system of decapod cephalopods: Eye muscles, eye muscle nerves and the oculomotor neurons in the central nervous system. *Phil. Trans. Roy. Soc. Lond. B* 340: 93–125.

Budelmann, B. U., Sachse, M., and Staudigl, M. (1987) The angular acceleration receptor system of *Octopus vulgaris*: Morphometry, ultrastructure and neuronal and synaptic organization. *Phil. Trans. Roy. Soc. Lond. B* 315: 305–343.

Budelmann, B. U., Riese, U., and Bleckmann, H. (1991) Structure, function, biological significance of the cuttlefish “lateral lines”. In E. Boucaud-Camou (ed.), *La Seiche. The Cuttlefish*. First International Symposium on the Cuttlefish, Sepia. Caen, June 1–3 1989. Caen, France: Institut de Bioclimie et de Biologie Appliquée, Université de Caen, pp. 201–209.

Budelmann, B. U., Schipp, R., and von Boletzky, S. (1997) Cephalopoda. In F. W. Harrison and A. J. Kohn (eds.), *Microscopic Anatomy of Invertebrates*. vol. 6A, *Mollusca II*. New York: Wiley-Liss, pp. 119–414.

Bult, R. and Mastebroek, H. A. K. (1994) Response characteristics of wide-field non-habituating non-directional motion-detecting neurons in the optic lobe of the locust, *Locusta migratoria*. *J. Comp. Physiol. A* 174: 723–729.

Buño, W., Chrispino, L., Monti-Bloch, L., and Mateos, A. (1981) Dynamic analysis of cockroach giant interneuron activity evoked by forced displacement of cercal thread-hair sensilla. *J. Neurobiol.* 12(6): 561–578.

Burdohan, J. A. and Comer, C. M. (1990) An antennal-derived mechanosensory pathway in the cockroach: Descending interneurons as a substrate for evasive behavior. *Brain Res.* 535: 347–352.

Burdohan, J. A. and Comer, C. M. (1996) Cellular organization of an antennal mechanosensory pathway in the cockroach *Periplaneta americana*. *J. Neurosci.* 16: 5830–5843.

Burghagen, H. and Ewert, J.-P. (1982) Question of “head preference” in response to worm-like dummies during prey-capture of toads *Bufo bufo*. *Behav. Processes* 7: 295–306.

Burghagen, H. and Ewert, J.-P. (1983) Influence of the background for discriminating object motion from self-induced motion in toads *Bufo bufo* (L.). *J. Comp. Physiol.* 152: 241–249.

Burkhardt, D. (1983) Wavelength perception and colour vision. *Symp. Soc. Exp. Biol.* 36: 371–397.

Burrows, M. (1996) *The Neurobiology of an Insect Brain*. London: Oxford Univ. Press.

Burrows, M. and Rowell, C. H. F. (1973) Connexions between descending visual interneurons and metathoracic motoneurons in the locust. *J. Comp. Physiol.* 85: 221–234.

Buxbaum-Conradi, H. and Ewert, J.-P. (1995) Pretecto-tectal influences I. What the toad's pretectum tells its tectum: An antidromic stimulation/recording study. *J. Comp. Physiol. A* 176: 169–180.

Buxbaum-Conradi, H. and Ewert, J.-P. (1999) Responses of single neurons in the toad's caudal ventral striatum to moving visual stimuli and test of their efferent projection by extracellular antidromic stimulation/recording techniques. *Brain Behav. Evol.* 54: 338–354.

Cakmak, I., Firatli, C., and Wells, H. (1998) The response of *Apis mellifera syriaca* and *A. m. armeniaca* to nectar differences. *Turk. J. Agri. Forestry* 22: 561–571.

Cakmak, I., Cook, P., Hollis, J., Shah, N., Huntley, D., van Valkenburg, D., and Wells, H. (1999) Africanized honey bee response to differences in reward frequency. *J. Apic. Res.* 38: 125–136.

Caldwell, R. L. and Dingle, H. (1975) Ecology and evolution of agonistic behavior in stomatopods. *Naturwissenschaften* 62: 214–222.

Caldwell, R. L. and Dingle, H. (1976) Stomatopods. *Sci. Am.* 234(1): 80–89.

Calkins, D. J. and Sterling, P. (1996) Absence of spectrally specific lateral inputs to midgut ganglion cells in primate retina. *Nature* 381: 613–615.

Camhi, J. M. (1988) Escape behavior in the cockroach: Distributed neural processing. *Experientia* 44(5): 401–408.

Camhi, J. M. and Levy, A. (1989) The code for stimulus direction in a cell assembly in the cockroach. *J. Comp. Physiol.* 165: 83–97.

Camhi, J. M. and Nolen, T. (1981) Properties of the escape system of cockroaches during walking. *J. Comp. Physiol.* 142: 339–346.

Camhi, J. M. and Tom, W. (1978) The escape behavior of the cockroach *Periplaneta americana*. I. Turning response to wind puffs. *J. Comp. Physiol.* 128: 193–201.

Camhi, J. M., Tom, W., and Volman, S. (1978) The escape behavior of the cockroach *Periplaneta americana*. II. Detection of natural predators by air displacement. *J. Comp. Physiol.* 128: 203–212.

Carpenter, R. H. S. (1988) *Movements of the Eyes*. London: Pion.

Cavanagh, P. (1991) What's up in top-down processing? In A. Gorea (ed.), *Representation of Vision—Trend and Tacit Assumptions in Vision Research*. Cambridge: Cambridge Univ. Press, pp. 295–304.

Cervantes-Pérez, F. (1989) Schema theory as a common language to study sensori-motor coordination. In J.-P. Ewert and M. A. Arbib (eds.), *Visuomotor Coordination: Amphibians, Comparisons, Models and Robots*. New York: Plenum, pp. 421–450.

Chapman, A. M. and Debski, E. A. (1995) Neuropeptide Y immunoreactivity of a projection from the lateral thalamic nucleus to the optic tectum of the leopard frog. *Vison Neurosci.* 12: 1–9.

Chapuis, N. (1987) Detour and shortcut abilities in several species of mammals. In P. Ellen and C. Thinus-Blanc (eds.), *Cognitive Processes and Spatial Orientation in Animals and Man*. Dordrecht, Netherlands: Martinus Nijhoff, pp. 97–106.

Cheng, K., Collett, T. S., Pickhard, A., and Wehner, R. (1987) The use of visual landmarks by honeybees: Bees weight landmarks according to their distance from the goal. *J. Comp. Physiol. A* 161: 469–475.

Chevalier, G. and Deniau, J. M. (1990) Disinhibition as a basic process in the expression of striatal functions. *Trends Neurosci.* 13: 277–280.

Chiao, C. C. and Hanlon, R. T. (2001) Cuttlefish camouflage: Visual perception of size, contrast and number of white squares on artificial checkerboard substrata initiates disruptive coloration. *J. Exp. Biol.* 204: 2119–2467.

Chiao, C. C., Cronin, T. W., and Marshall, J. (2000) Eye design and color signaling in a stomatopod crustacean, *Gonodactylus smithii*. *Brain Behav. Evol.* 56: 107–122.

Chittka, L. (1992) The color hexagon: A chromaticity diagram based on photoreceptor excitations as a generalized representation of colour opponency. *J. Comp. Physiol. A* 170: 533–543.

Chittka, L. (1996) Optimal sets of color receptors and color opponent systems for coding of natural objects in insect vision. *J. Theor. Biol.* 181: 179–196.

Chittka, L. (1998) Sensorimotor learning in bumblebees: Long-term retention and reversal training. *J. Exp. Biol.* 201: 515–524.

Chittka, L. (1999) Bees, white flowers and the color hexagon—a reassessment? No, not yet. *Naturwissenschaften* 86: 595–597.

Chittka, L. (2002) Influence of intermittent rewards in learning to handle flowers in bumblebees. *Entomol. General* 26: 85–91.

Chittka, L. and Briscoe, A. (2001) Why sensory ecology needs to become more evolutionary—insect color vision as a case in point. In F. G. Barth and A. Schmid (eds.), *Ecology of Sensing*. Berlin: Springer-Verlag, pp. 19–37.

Chittka, L. and Geiger, K. (1995) Can honey bees count landmarks? *Anim. Behav.* 49: 159–164.

Chittka, L. and Menzel, R. (1992) The evolutionary adaptation of flower colors and the insect pollinators' color vision systems. *J. Comp. Physiol. A* 171: 171–181.

Chittka, L. and Thomson, J. D. (1997) Sensori-motor learning and its relevance for task specialization in bumble bees. *Behav. Ecol. Sociobiol.* 41: 385–398.

Chittka, L. and Waser, N. M. (1997) Why red flowers are not invisible for bees. *Isr. J. Plant Sci.* 45: 169–183.

Chittka, L., Beier, W., Hertel, H., Steinmann, E., and Menzel, R. (1992) Opponent colour coding is a universal strategy to evaluate the photoreceptor inputs in Hymenoptera. *J. Comp. Physiol. A* 170: 545–563.

Chittka, L., Vorobyev, M., Shmida, A., and Mezel, R. (1993) Bee colour vision—The optimal system for the discrimination of flower colours with three spectral photoreceptor types? In K. Wiese (ed.), *Sensory Systems of Arthropods*. Basel: Switzerland: Birkhaeuser Verlag, pp. 211–218.

Chittka, L., Shmida, A., Troje, N., and Menzel, R. (1994) Ultraviolet as a component of flower reflections and the colour perception of hymenoptera. *Vison Res.* 34: 1489–1508.

Chittka, L., Kunze J., and Geiger, K. (1995) The influences of landmarks on distance estimation of honeybees. *Anim. Behav.* 50: 23–31.

Chittka, L., Thomson, J. D., and Waser, N. M. (1999) Flower constancy, insect psychology and plant evolution. *Naturwissenschaften* 86: 361–377.

Chittka, L., Spaethe, J., Schmidt, A., and Hickelsberger, A. (2001) Adaptation, constraint and chance in the evolution of flower color and pollinator color vision. In L. Chittka and J. D. Thomson (eds.), *Cognitive Ecology of Pollination*. Cambridge: Cambridge Univ. Press, pp. 106–126.

Chou, W. H., Huber, A., Bentrop, J., Schulz, S., Schwab, K., Chadwell, L. V., Paulsen, R., and Britt, S. G. (1999) Patterning of the R7 and R8 photoreceptor cells of *Drosophila*: Evidence for induced and default cell-fate specification. *Development* 126: 607–616.

Clairambault, P. (1976) Development of the prosencephalon. In R. Llinás and W. Precht (eds.), *Frog Neurobiology*. Berlin: Springer-Verlag, pp. 924–945.

Clark, R. J. and Jackson, R. R. (1994a) *Portia labiata*, a cannibalistic jumping spider, discriminates between own and foreign eggsacs. *Int. J. Comp. Psychol.* 7: 38–43.

Clark, R. J. and Jackson, R. R. (1994b) Self-recognition in a jumping spider: *Portia labiata* females discriminate between their own draglines and those of conspecifics. *Ethol. Ecol. Evol.* 6: 371–375.

Clark, R. J. and Jackson, R. R. (1995a) Dragline-mediated sex recognition in two species of jumping spider (Araneae: Salticidae), *Portia labiata* and *Portia fimbriata*. *Ethol. Ecol. Evol.* 7: 73–77.

Clark, R. J. and Jackson, R. R. (1995b) Araneophagic jumping spiders discriminate between the draglines of familiar and unfamiliar conspecifics. *Ethol. Ecol. Evol.* 7: 185–190.

Clark, R. J. and Jackson, R. R. (2000) Web use during predatory encounters between *Portia fimbriata*, an araneophagic jumping spider and its preferred prey, other jumping spiders. *NZ J. Zool.* 27: 129–136.

Clark, R. J., Jackson, R. R., and Harland, D. P. (2001) Speculative hunting by an araneophagic salticid spider. *Behavior* 137: 1601–1612.

Cleal, K. and Prete, F. R. (1996) The predatory strike of free ranging praying mantises, *Sphodromantis lineola* (Burr.). II: Strikes in the horizontal plane. *Brain Behav. Evol.* 48: 191–204.

Clutton-Brock, T. M. and Harvey, P. H. (1980) Primates, brains and ecology. *J. Zool. Lond.* 190: 309–323.

Cobb, C. S., Pope, S. K., and Williamson, R. (1995a) Circadian rhythms to light-dark cycles in the lesser octopus, *Eledone cirrhosa*. *Mar. Freshwater Behav. Physiol.* 26: 47–57.

Cobb, C. S., Williamson, R., and Pope, S. K. (1995b) The responses of the epistellar photoreceptors to light and their effect on circadian rhythms in the lesser octopus, *Eledone cirrhosa*. *Mar. Freshwater Behav. Physiol.* 26: 59–69.

Cohen, A. I. (1973) An ultrastructural analysis of the photoreceptors of the squid and their synaptic connections. II. Intraretinal synapses and plexus. *J. Comp. Neurol.* 147: 379–398.

Cohen, M. J. (1964) The peripheral organisation of sensory systems. In R. F. Reiss (ed.), *Neural Theory and Modeling*. Stanford, Calif.: Stanford University Press, pp. 273–292.

Colborn, M., Ahmad-Annuar, A., Fauria K., and Collett, T. S. (1999) Contextual modulation of visuomotor associations in bumble-bees (*Bombus terrestris*). *Proc. Roy. Soc. Lond. B* 266 (1436): 2413–2418.

Collett, T. S. (1977) Stereopsis in toads. *Nature* 267: 349–351.

Collett, T. S. (1982) Do toads plan detours? A study of the detour behaviour of *Bufo viridis*. *J. Comp. Physiol.* 146: 261–271.

Collett, T. S. (1983) Picking a route: Do toads follow rules or make plans? In J.-P. Ewert, R. R. Capranica, and D. J. Ingle (eds.), *Advances in Vertebrate Neuroethology*. New York: Plenum, pp. 321–330.

Collett, T. S. (1996) Insect navigation en route to the goal—multiple strategies for the use of landmarks. *J. Exp. Biol.* 199: 227–235.

Collett, T. S. and Cartwright, B. A. (1983) Eidetic images in insects: Their role in navigation. *Trends Nevrosci.* 6: 101–105.

Collett, T. S. and Kelber, A. (1988) The retrieval of visuo-spatial memories by honeybees. *J. Comp. Physiol. A* 163: 145–150.

Collett, T. S., Fry, S. N., and Wehner, R. (1993) Sequence learning by honeybees. *J. Comp. Physiol. A* 172: 693–706.

Comer, C. M. (1985) Analyzing cockroach escape behavior with lesions of individual giant interneurons. *Brain Res.* 335: 342–346.

Comer, C. M. (1987) Sensorimotor functions: What is a command, that a code may yield it? A commentary. *Behav. Brain Sci.* 10: 372.

Comer, C. M. and Dowd, J. P. (1993) Multisensory processing for movement: Antennal and cercal mediation of escape turning in the cockroach. In R. D. Beer, R. E. Ritzmann, and T. McKenna (eds.), *Biological Neural Networks in Invertebrate Neuroethology and Robotics*. New York: Academic Press, pp. 89–112.

Comer, C., Schotland, J., and Grobstein, P. (1985) Short and longterm effects of unilateral vestibular lesions on posture and orienting movements in the frog. *Soc. Neurosci. Abstr.* 11: 289.

Comer, C. M., Dowd, J. P., and Stubblefield, G. (1988) Escape responses following elimination of the giant interneuron pathway in the cockroach, *Periplaneta americana*. *Brain Res.* 445: 370–375.

Comer, C. M., Mara, E., Murphy, K. A., Getman, M., and Mungy, M. C. (1994) Multisensory control of escape in the cockroach *Periplaneta americana* II. Patterns of touch-evoked behavior. *J. Comp. Physiol.* 174: 13–26.

Comer, C. M., Parks, L., Halvorsen, M. B., and Breese-Terteling, A. (2003) The antennal system and cockroach evasive behavior II: Stimulus identification and localization are separable antennal functions. *J. Comp. Physiol. A* 189: 97–103 (in press).

Cooper, R. L., Li, H., Cole, J. E., and Hopper, H. L. (1998) The neuroecology of cave crayfish: Behavioral and anatomical comparisons of vision in blind epigian species raised in a cave and troglobitic species. *Abst. Soc. Neurosci.* 24: 468.10.

Cott, H. B. (1936) The effectiveness of protective adaptations in the hive-bee, illustrated by experiments on the feeding reactions, habit formation and memory of the common toad (*Bufo bufo bufo*). *Proc. Zool. Soc.* (*Lond.*) 1: 113–133.

Crane, J. (1949) Comparative biology of salticid spiders at Rancho Grande, Venezuela. Part IV. An analysis of display. *Zoolologica, New York* 34: 159–214.

Cronin, T. W. (1985) The visual pigment of a stomatopod crustacean, *Squilla empusa*. *J. Comp. Physiol.* 156: 679–687.

Cronin, T. W. (1986) Optical design and evolutionary adaptation in crustacean compound eyes. *J. Crust. Biol.* 6: 1–23.

Cronin, T. W. (1994) Polychromatic vision in mantis shrimps. *Sensornie Systemy* 8: 95–106.

Cronin, T. W. and Caldwell, R. L. (2002) Tuning of visual function in three mantis shrimp species that inhabit a range of depths. I: Visual pigments. *J. Comp. Physiol. A* 188: 179–186.

Cronin, T. W. and Goldsmith, T. H. (1981) Fluorescence of crayfish metarhodopsin studied in single rhabdoms. *Biophys. J.* 35: 653–664.

Cronin, T. W. and Marshall, N. J. (1989a) Multiple spectral classes of photoreceptors in the retinas of gonodactyloid stomatopod crustaceans. *J. Comp. Physiol. A* 166: 267–275.

Cronin, T. W. and Marshall, N. J. (1989b) A retina with at least ten spectral types of photoreceptors in a stomatopod crustacean. *Nature* 339: 137–140.

Cronin, T. W. and Marshall, N. J. (2001) Parallel processing and image analysis in the eyes of mantis shrimps. *Biol. Bull.* 200: 177–183.

Cronin, T. W. and Shashar, N. (2001) The linearly polarized light field in clear, tropical marine waters: Spatial and temporal variation of light intensity, degree of polarization and e-vector angle. *J. Exp. Biol.* 204: 2461–2467.

Cronin, T. W., Nair, J. N., Doyle, R. D., and Caldwell, R. L. (1988) Visual tracking of rapidly moving targets by stomatopod crustaceans. *J. Exp. Biol.* 138: 155–179.

Cronin, T. W., Marshall, N. J., and Land, M. F. (1991) Optokinesis in gonodactyloid mantis shrimps (Crustacea; Stomatopoda; Gonodactylidae). *J. Comp. Physiol. A* 168: 233–240.

Cronin, T. W., Yan, H. Y., and Bidle, K. D. (1992) Regional specialization for control of ocular movements in the compound eyes of a stomatopod crustacean. *J. Exp. Biol.* 171: 373–393.

Cronin, T. W., Marshall, N. J., and Caldwell, R. L. (1993) Photoreceptor spectral diversity in the retinas of squilloid and lysiosquilloid stomatopod crustaceans. *J. Comp. Physiol. A* 172: 339–350.

Cronin, T. W., Marshall, N. J., and Caldwell, R. L. (1994a) The intrarhabdomal filters in the retinas of mantis shrimps. *Vison Res.* 34: 279–291.

Cronin, T. W., Marshall, N. J., and Caldwell, R. L. (1994b) The retinas of mantis shrimps from low-light environments (Crustacea; Stomatopoda; Gonodactylidae). *J. Comp. Physiol. A* 174: 607–619.

Cronin, T. W., Marshall, N. J., and Land, M. F. (1994c) Vision in mantis shrimps. *Am. Sci.* 82: 356–365.

Cronin, T. W., Marshall, N. J., Caldwell, R. L., and Shashar, N. (1994d) Specialization of retinal function in the compound eyes of mantis shrimps. *Vison Res.* 34: 2639–2656.

Cronin, T. W., Marshall, N. J., Quinn, C. A., and King, C. A. (1994e) Ultraviolet photoreception in mantis shrimp. *Vison Res.* 34: 1443–1452.

Cronin, T. W., Shashar, N., and Wolff, L. (1995) Imaging technology reveals the polarized light fields that exist in nature. *Biophotonics Int.* 2: 38–41.

Cronin, T. W., Marshall, N. J., and Caldwell, R. L. (1996) Visual pigment diversity in two genera of mantis shrimps implies rapid evolution. *J. Comp. Physiol. A* 179: 371–384.

Cronin, T. W., Marshall, N. J., and Caldwell, R. L. (2000) Spectral tuning and the visual ecology of mantis shrimps. *Phil. Trans. Roy. Soc. B* 355: 1263–1267.

Cronin, T. W., Caldwell, R. L., and Marshall, N. J. (2001) Tunable colour vision in a mantis shrimp. *Nature* 411: 547–548.

Cronin, T. W., Caldwell, R. L., and Erdmann, M. (2002) Tuning of visual function in three mantis shrimp species that inhabit a range of depths. II: Filter pigments. *J. Comp. Physiol. A* 188: 187–197.

Cummins, D. and Goldsmith, T. H. (1981) Cellular identification of the violet receptor in the crayfish eye. *J. Comp. Physiol. A* 142: 199–202.

Curio, E. (1976) *The Ethology of Predation.* Berlin: Springer-Verlag.

Cutting, J. E., Moore, C., and Morrison, R. (1988) Masking the motions of human gait. *Percept. Psychophys.* 44: 339–347.

Dacke, M., Nilsson, D. E., Warrant, E. J., Blest, A. D., Land, M. F., and O'Carroll, D. C. (1999) Built-in polarizers form part of a compass organ in spiders. *Nature* 401: 470–473.

Dafni, A., Bernhardt, P., Shmida, A., Ivri, Y., Greenbaum, S., O'Toole, C., and Losito L. (1990) Red bowl-shaped flowers: Convergence for beetle pollination in the Mediterranean region. *Isr. J. Bot.* 39: 81–92.

Dale, R. H. I. (1988) Spatial memory in pigeons on a four-arm radial maze. *Can. J. Psychol.* 42: 78–83.

Daley, D. L. and Camhi, J. M. (1988) Connectivity pattern of the cercal-to-giant interneuron system of the American cockroach. *J. Neurophysiol.* 60: 1350–1368.

Daley, D. L. and Delcomyn, F. (1980) Modulation of excitability of cockroach giant interneurons during walking I. Simultaneous excitation and inhibition. *J. Comp. Physiol.* 138: 231–239.

Daley, D. L., Vardi, N., Appignani, B., and Camhi, J. M. (1981) Morphology of the giant interneurons and cercal nerve projections of the American cockroach. *J. Comp. Neurol.* 196(1): 41–52.

D'Amato, M. R., Salmon, D. P., and Colombo, M. (1985) Extent and limits of the matching concept in monkeys (*Cebus apella*). *J. Exp. Psychol. Anim. Behav. Proc.* 11: 35–51.

D'Aniello, B., Vallarino M., Pinelli C., Fiorentiono, M., and Rastogi, K. R. (1996) Neuropeptide Y: Localization in the brain and pituitary of the developing frog (*Rana esculenta*). *Cell Tiss. Res.* 285: 253–259.

Darwin, C. (1871) *The Descent of Man and Selection in Relation to Sex*. London: John Murray.

Davis, W. J. (1971) The integrative action of nervous system in crustacean equilibrium reactions. In S. A. Gordon and M. J. Cohen (eds.), *Gravity and Organism*. Chicago: Univ. of Chicago Press, pp. 237–250.

Dawkins, R. (1996) *Climbing Mount Improbable*. New York: W. W. Norton.

de Couet, H. G. and Sigmund, D. (1985) Monoclonal antibodies to crayfish rhodopsin. I. Biochemical characterization and crossreactivity. *Eur. J. Cell Biol.* 38: 106–112.

de Souza, J., Hertel, H., Ventura, D. F., and Menzel, R. (1992) Response properties of stained monopolar cells in the honeybee lamina. *J. Comp. Physiol. A* 170: 267–274.

Dean, J. (1980a) Encounters between bombardier beetles and two species of toads (*Bufo americanus*, *B. marinus*): Speed of prey-capture does not determine success. *J. Comp. Physiol.* 135: 41–50.

Dean, J. (1980b) Effects of thermal and chemical components of bombardier beetle chemical defense: Glossopharyngeal response in two species of toads (*Bufo americanus*, *B. marinus*). *J. Comp. Physiol.* 135: 51–59.

Dean, P. and Redgrave, P. (1991) Approach and avoidance systems in the rat. In M. A. Arbib and J.-P. Ewert (eds.), *Visual Structures and Integrated Functions*. Berlin: Springer-Verlag, pp. 191–204.

Dean, P., Redgrave, P., and Mitchell, I. J. (1988a) Organization of efferent projections from superior colliculus to brainstem in rat: Evidence for functional output channels. *Prog. Brain Res.* 75: 27–36.

Dean, P., Redgrave, P., and Westby, G. W. (1988b) Event or emergency? Two response systems in the mammalian superior colliculus. *Trends Neurosci.* 12: 137–147.

Deeb, S. S. and Motulsky, A. G. (1996) Molecular genetics of human color vision. *Behav. Genet.* 26: 195–207.

Deely, J. (2001) “A sign is what?” *Sign System Studies* 29: 705–744.

Dennett, D. C. (1991) *Consciousness Explained*. London: Penguin.

Dennett, D. C. (1995) Animal consciousness: What matters and why. *Soc. Res.* 62: 691–710.

Dennett, D. C. (1996) *Kinds of minds: Towards an Understanding of Consciousness*. New York: Simon and Schuster.

Denton, E. J. (1970) On the organization of reflecting surfaces in some marine animals. *Phil. Trans. Roy. Soc. Lond. B* 258: 285–313.

Denton, E. J. and Land, M. F. (1971) Mechanism of reflexion in silvery layers of fish and cephalopods. *Proc. Roy. Soc. Lond. B* 178: 43–61.

Denton, E. J. and Locket, N. A. (1989) Possible wavelength discrimination by multi-bank retinae in the deep-sea fishes. *J. Mar. Biol. Assoc. UK* 69: 409–435.

Desimone, R. (1998) Visual attention mediated by biased competition in extrastriate visual cortex. *Phil. Trans. Roy. Soc. Lond. B* 353: 1245–1255.

DeVoe, R. D. (1975) Ultraviolet and green receptors in principal eyes of jumping spiders. *J. Gen. Physiol.* 66: 193–207.

Dicke, U. (1999) Morphology, axonal projection pattern and response types of tectal neurons in plethodontid salamanders. I: Tracer study of projection neurons and their pathways. *J. Comp. Neurol.* 404: 473–488.

Dicke, U. and Roth, G. (1996) Similarities and differences in the cytoarchitecture of the tectum of frogs and salamanders. *Acta. Biol. Hung.* 47: 41–59.

Dicke, U., Roth, G., and Matsushima, T. (1998) Neural substrate for motor control of feeding in amphibians. *Acta Anat.* 163: 127–143.

DiDomenico, R. and Eaton, R. C. (1987) Toward a reformulation of the command concept. *Behav. Brain Sci.* 10: 374–375.

Dirsh, V. M. (1965) Revision of the family Pneumoridae (Orthoptera: Acridoidea). *Bull. Br. Mus.* (*Nat. Hist.*) *Entomol.* 15: 325–396.

Disse, D., Ewert, J. C., Hesebeck, O., and Langer, F. (1992) ODANN: Objekt dimensionieren mit ANN. *Abt. Neurobiologie*, University of Kassel.

Dole, J. W., Rose, B. B., and Tachiki, K. H. (1981) Western toads (*Bufo boreas*) learn odor of prey insects. *Herpetologia* 37: 63–68.

Dominy, N. J. and Lucas, P. W. (2001) Ecological importance of trichromatic vision to primates. *Nature* 410: 363–366.

Doty, R. W. (1987) Has the greedy toad lost its soul and if so, what was it? *Behav. Brain Sci.* 10: 375.

Dowd, J. P. and Comer, C. M. (1988) The neural basis of orienting behavior: A computational approach to the escape turn of the cockroach. *Biol. Cybernet.* 60: 37–48.

Drees, O. (1952) Untersuchungen uber die angeborenen Verhaltensweisen bei Springspinnen (Salticidae). *Z. Tierpsychol.* 9: 169–207.

Dukas, R. (1998) Introduction. In R. Dukas (ed.), *Cognitive Ecology: The Evolutionary Ecology of Information Processing and Decision Making*. Chicago: Univ. of Chicago Press.

Dumpert, K. and Gnatzy, W. (1977) Cricket combined mechanoreceptors and kicking response. *J. Comp. Physiol.* 122: 9–25.

Dunham, P. J. (1978) Sex pheromones in crustacea. *Biol. Rev.* 53: 555–583.

Dunham, P. J. (1988) Pheromones and behavior in Crustacea. In H. Laufer and G. H. Downer (eds.), *Endocrinolgy of Selected Invertebrate Types*. New York: Alan R. Liss, pp. 375–392.

Dyer, A. G. (1998) The colour of flowers in spectrally variable illumination and insect pollinator vision. *J. Comp. Physiol. A* 183: 203–212.

Dyer, A. G. (1999) Broad spectral sensitivities in the honeybee's photoreceptors limit colour constancy. *J. Comp. Physiol. A* 185: 445–453.

Dyer, A. G. and Chittka, L. (2004) Biological significance of discriminating between similar colours in spectrally variable illumination: bumblebees as a study case. *J. Comp. Physiol. A*, 190: 105–114.

Eakin, R. M. and Brandenburger, J. L. (1971) Fine structure of the eyes of jumping spiders. *J. Ultrastruct. Res.* 37: 618–663.

Eaton, R. C. (2001) The Mauthner cell and other identified neurons of the brainstem escape network of fish. *Prog. Neurobiol.* 63: 467–485.

Ebbesson, S. O. E. (1980a) *Comparative Neurology of the Telencephalon*. New York: Plenum.

Ebbesson, S. O. E. (1980b) The parcellation theory and its relation to interspecific variability in brain organization, evolutionary and ontogenetic development and neuronal plasticity. *Cell Tiss. Res.* 213: 179–212.

Ebbesson, S. O. E. (1984) Evolution and ontogeny of neural circuits. *Behav. Brain Sci.* 7: 321–366.

Ebbesson, S. O. E. (1987) Prey-catching in toads: An exceptional neuroethological model. *Behav. Brain Sci.* 10: 375–376.

Ebrey, T. G. (1977) New wavelength dependent visual pigment nomograms. *Vision Res.* 17: 147–151.

Edmunds, M. (1972) Defensive behaviour in Ghanaian praying mantids. *Zool. J. Linn. Soc.* 51: 1–32.

Edmunds, M. and Brunner, D. (1999) Ethology of defenses against predators. In F. R. Prete, H. Wells, P. Wells, and L. E. Hurd (eds.), *The Praying Mantids*. Baltimore, Md.: Johns Hopkins Univ. Press, pp. 276–299.

Edrich, W., Neumeyer, C., and von Helversen, O. (1979) "Anti-sun orientation" of bees with regard to a field of ultraviolet light. *J. Comp. Physiol. A* 134: 151–157.

Edwards, D. H. (1982) The cockroach DCMD neurone. II. Dynamics of response habituation and convergence of spectral inputs. *J. Exp. Biol.* 99: 91–107.

Edwards, D. H., Heitler, W. J., and Krasne, F. B. (1999) Fifty years of a command neuron: The neurobiology of escape behavior in the crayfish. *Trends Newrosci.* 22(4): 153–161.

Edwards, J. S. (1997) The evolution of insect flight: Implications for the evolution of the nervous system. *Brain Behav. Evol.* 50: 8–12.

Edwards, J. S. and Palka, J. (1974) The cerci and abdominal giant fibres of the house cricket, *Acheta domesticus*. I. Anatomy and physiology of normal adults. *Proc. Roy. Soc. Lond. B* 185(78): 83–103.

Edwards, J. S. and Palka, J. (1991) Insect neural evolution—a fugue or an opera? *Sem. Neurosci.* 3: 391–398.

Edwards, J. S. and Reddy, R. (1986) Mechanosensory appendages and giant interneurons in the firebrat (*Thermobia domestica*, Thysanura): A prototype system for predator evasion. *J. Comp. Neurol.* 243: 535–546.

Egelhaaf, M. and Borst A. (1990) Bewegungswahrnehmung und visuelle Orientierung bei Fliegen. *Naturwissenschaften* 77: 366–377.

Eggleton, P. (2001) Termites and trees: A review of recent advances in termite phylogenetics. *Insectes Sociaux* 48: 187–193.

Eguchi, E. and Waterman, T. H. (1966) Fine structure patterns in crustacean rhabdoms. In C. G. Bernhard (ed.), *The Functional Organization of the Compound Eye*. Oxford: Pergamon Press, pp. 105–124.

Ehn, R. and Tichy, H. (1994) Hygro- and thermoreceptive tarsal organ in the spider *Cupiennius salei*. *J. Comp. Physiol. A* 174: 345–350.

Eibl-Eibesfeldt, I. (1951) Nahrungserwerb und Beuteschema der Erdkröte (*Bufo bufo* L.). *Behaviour* 4: 1–35.

Eisenberg, J. F. and Wilson, D. E. (1978) Relative brain size and feeding strategies in Chiroptera. *Evolution* 32: 740–751.

Endler, J. A. (1990) On the measurement and classification of colour in studies of animal colour patterns. *Biol. J. Linn. Soc.* 41: 315–352.

Endler, J. A. (1992) Signals, signal conditions and the direction of evolution. *Am. Nat.* 139: S125–S153.

Endler, J. A. (1993) The color of light in forests and its implications. *Ecol. Monogr.* 63: 1–27.

Endler, J. A., Basolo, A., Glowacki, S., and Zerr, J. (2001) Variation in response to artificial selection for light sensitivity in guppies (*Poecilia reticulata*). *Am. Nat.* 158: 36–48.

Epstein, R. (1982) Representation: A concept that fills no gaps. *Behav. Brain Sci.* 5: 377–378.

Ewert, J.-P. (1968) Der Einfluss von Zwischenhirndefekten auf die Visuomotorik im Beutefang- und Fluchtverhalten der Erdkröte (*Bufo bufo* L.). *Z. Vergl. Physiol.* 61: 41–70.

Ewert, J.-P. (1971) Single unit response of the toad (*Bufo americanus*) caudal thalamus to visual objects. *Z. Vergl. Physiol.* 74: 81–102.

Ewert, J.-P. (1974) The neural basis of visually guided behavior. *Sci. Am.* 230: 34–42.

Ewert, J.-P. (1984) Tectal mechanisms that underlie prey-catching and avoidance behaviors in toads. In H. Vanegas (ed.), *Comparative Neurology of the Optic Tectum*. New York: Plenum, pp. 247–416.

Ewert, J.-P. (1987) Neuroethology of releasing mechanisms: Prey catching in toads. *Behav. Brain Sci.* 10: 337–405.

Ewert, J.-P. (1992) Neuroethology of an object features-relating algorithm and its modification by learning. *Rev. Neurosci.* 3: 45–63.

Ewert, J.-P. (1997) Neural correlates of key stimulus and releasing mechanism: A case study and two concepts. *Trends Neurosci.* 20: 332–339.

Ewert, J.-P. (2002) Command neurons and command systems. In M. A. Arbib (ed.), *The Handbook of Brain Theory and Neural Networks*, 2nd ed. Cambridge, Mass.: MIT Press, pp. 233–238.

Ewert, J.-P. and Borchers, W. (1974) Antworten retinaler Ganglienzellen bei freibeweglichen Kröten. *J. Comp. Physiol.* 92: 117–130.

Ewert, J.-P. and Hock, F. J. (1972) Movement sensitive neurones in the toad's retina. *Exp. Brain Res.* 16: 41–59.

Ewert, J.-P. and Traud, R. (1979) Releasing stimuli for antipredator behaviour in the common toad, *Bufo bufo* (L.). *Behaviour* 68: 170–180.

Ewert, J.-P. and von Seelen, W. (1974) Neurobiologie und System-Theorie eines visuellen Muster-Erkennungsmechanismus bei Kröten. *Kybernetik* 14: 167–183.

Ewert, J.-P., Burghagen, H., and Schürg-Pfeiffer, E. (1983) Neuroethological analysis of the innate releasing mechanism for prey-catching behavior in toads. In J.-P. Ewert, R. R. Capranica, and D. J. Ingle (eds.), *Advances in Vertebrate Neuroethology*. New York: Plenum, pp. 413–475.

Ewert, J.-P., Framing, E. M., Schürg-Pfeiffer, E., and Weerasuriya, A. (1990) Responses of medullary neurons to moving visual stimuli in the common toad: I. Characterization of medial reticular neurons by extracellular recording. *J. Comp. Physiol. A* 167: 495–508.

Ewert, J.-P., Dinges, A. W., and Finkenstädt, T. (1994a) Species-universal stimulus responses, modified through conditioning, re-appear after telencephalic lesions in toads. *Naturwissenschaften* 81: 317–320.

Ewert, J.-P., Beneke, T. W., Schürg-Pfeiffer, E., Schwippert, W. W., and Weerasuriya, A. (1994b) Sensorimotor processes that underlie feeding behavior in tetrapods. In V. L. Bels, M. Chardon, and P. Vandevalle (eds.), *Advances in Comparative and Environmental Physiology*. vol. 18, *Biomechanics of Feeding in Vertebrates*. Berlin: Springer-Verlag, pp. 119–161.

Ewert, J.-P. and Borchers, H.-W. (1971) Reaktionscharakteristik von Neuronen aus dem Tectum opticum und Subtectum der Erdkröte *Bufo bufo* (L.). *Z. Vergl. Physiol.* 71: 165–189.

Ewert, J.-P. and Kehl, W. (1978) Configurational prey-selection by individual experience in the toad *Bufo bufo*. *J. Comp. Physiol. A* 126: 105–114.

Ewert, J.-P., Schürg-Pfeiffer, E., and Schwippert, W. W. (1996) Influence of pretectal lesions on tectal responses to visual stimulation in anurans: Field potential, single neuron and behavior analyses. *Acta Biol. Acad. Sci. Hung.* 47: 223–245.

Ewert, J.-P., Buxbaum-Conradi, H., Dreisvogt, F., Glagow, M., Merkel-Harff, C., Röttgen, A., Schürg-Pfeiffer, E., and Schwippert, W. W. (2001) Neural modulation of visuomotor functions underlying prey-catching behaviour in anurans: Perception, attention, motor performance, learning. *Comp. Biochem. Physiol. A* 128: 417–461.

Exner, S. (1891) *Die Physiologie der Facettirten Augen von Krebsen und Insecten*. Leipzig, Vienna: Deuticke.

Fabre, J.-H. (1912) *Social Life in the Insect World*. (transl. B. Miall) London: T. Fisher Unwin.

Fagan, W. F. and Hurd, L. E. (1994) Hatch density variation of a generalist arthropod predator: Population consequences and community impact. *Ecology* 75: 2022–2032.

Fent, K. (1986) Polarized skylight orientation in the desert ant *Cataglyphis*. *J. Comp. Physiol. A* 158: 145–150.

Ferguson, G. P., Messenger, J. B., and Budelmann, B. U. (1994) Gravity and light influence the countershading reflexes of the cuttlefish *Sepia officinalis*. *J. Exp. Biol.* 191: 247–256.

Field, L. H. (1991) Mechanism for range fractionation in chordotonal organs of *Locusta migratoria* (L) and Valanga sp. (Orthoptera: Acrididae). *Int. J. Insect. Morphol. Embryol.* 20: 25–39.

Finkenstädt, T. (1989) Visual associative learning: Searching for behaviorally relevant brain structures in toads. In J.-P. Ewert and M. A. Arbib (eds.), *Visuomotor Coordination: Amphibians, Comparisons, Models and Robots*. New York: Plenum, pp. 799–832.

Finkenstädt, T. and Ewert, J.-P. (1983a) Processing of area dimensions of visual key stimuli by tectal neurons in *Salamandra salamandra*. *J. Comp. Physiol.* 153: 85–98.

Finkenstädt, T. and Ewert, J.-P. (1983b) Visual pattern discrimination through interactions of neural networks: A combined electrical brain stimulation, brain lesion and extracellular recording study in *Salamandra salamandra*. *J. Comp. Physiol.* 153: 99–110.

Finkenstädt, T. and Ewert, J.-P. (1985) Glucose utilization in the toad's brain during anesthesia and stimulation of the ascending reticular arousal system: A ^{14}C-2-deoxyglucose study. *Naturwissenschaften* 72: 161–162.

Finkenstädt, T. and Ewert, J.-P. (1988) Stimulus-specific long-term habituation of visually guided orienting behavior toward prey in toads: A ^{14}C-2DG study. *J. Comp. Physiol. A* 163: 1–11.

Finkenstädt, T. and Ewert, J.-P. (1992) Localization of learning-related metabolical changes in brain structures of common toads: A 2-DG-study. In F. Gonzalez-Lima, T. Finkenstädt, and H. Scheich (eds.), *Advances in Metabolic Mapping Techniques for Brain Imaging of Behavioral and Learning Functions*. Dordrecht, Netherlands: Kluwer, pp. 409–445.

Finkenstädt, T., Adler, N. T., Allen, T. O., Ebbesson, S. O. E., and Ewert, J.-P. (1985) Mapping of brain activity in mesencephalic and diencephalic structures of toads during presentation of visual key stimuli: A computer-assisted analysis of 14C-2DG autoradiographs. *J. Comp. Physiol. A* 156: 433–445.

Finkenstädt, T., Adler, N. T., Allen, T. O., and Ewert, J.-P. (1986) Regional distribution of glucose utilization in the telencephalon of toads in response to configurational visual stimuli: A 14C-2DG study. *J. Comp. Physiol. A* 158: 457–467.

Flores, E. E. C. (1983) Visual discrimination testing in the squid *Todarodes pacificus*: Experimental evidence for lack of color vision. *Mem. Nat. Hist. Mus. Victoria* 44: 213–227.

Foelix, R. F. (1996) *Biology of Spiders*. New York: Oxford Univ. Press and Georg Thieme Verlag.

Fonseca, P. J., Münch, D., and Hennig, R. M. (2000) How cicadas interpret acoustic signals. *Nature* 405: 297–298.

Foreman, N. and Stevens, R. (1987) Relationships between the superior colliculus and hippocampus: Neural and behavioral considerations. *Behav. Brain Sci.* 10: 101–151.

Forrest, T. G. and Green, D. M. (1991) Sexual selection and female choice in mole crickets (Scapteriscus: Gryllotalpidae): Modeling the effects of intensity and male spacing. *Bioacoustics* 3: 93–109.

Forster, L. M. (1979) Visual mechanisms of hunting behaviour in *Trite planiceps*, a jumping spider (Araneae: Salticidae). *NZ J. Zool.* 6: 79–93.

Forster, L. M. (1982a) Vision and prey-catching strategies in jumping spiders. *Am. Sci.* 70: 165–175.

Forster, L. M. (1982b) Visual communication in jumping spiders (Salticidae). In P. N. Witt and J. S. Rovner (eds.), *Spider Communication: Mechanisms and Ecological Significance*. Princeton, *N.J.: Princeton Univ.* Press, pp. 161–212.

Forster, L. M. (1985) Target discrimination in jumping spiders (Araneae: Salticidae) In F. G. Barth (ed.), *Neurobiology of Arachnids*. Berlin: Springer-Verlag, pp. 249–274.

Franceschini, N., Kirschfeld, K., and Minke, B. (1981) Fluorescence of photoreceptor cells observed in vivo. *Science* 213: 1264–1267.

Fraser, P. J. (1977) Cercal ablation modifies tethered flight behaviour of cockroach. *Nature* 268(5620): 523–524.

Frost, B. J. (1982) Mechanisms for discriminating object motion from self-induced motion in the pigeon. In D. J. Ingle, M. A. Goodale, and R. J. W. Mansfield (eds.), *Analysis of Visual Behavior*. Cambridge, Mass: MIT Press, pp. 177–196.

Fujimoto, K., Yanase, T., and Ishizuka, I. (1966) The visual substance of the crayfish, *Procambarus clarkii*. *Mem. Osaka Gakugi Univ.* 15B: 109–114.

Fukushi, T. (1990) Colour discrimination from various shades of grey in the trained blowfly, *Lucilia cuprina*. *J. Insect Physiol.* 36: 69–75.

Fülöp, A. and Menzel, R. (2000) Risk-indifferent foraging behaviour in honeybees. *Anim. Behav.* 60: 657–666.

Gabbiani. F., Krapp, H. G., and Laurent, G. (1999) Computation of object approach by a wide-field, motion-sensitive neuron. *J. Neurosci.* 19: 1122–1141.

Gadagkar, G., Srinivasan, M. V., and Zhang, S. W. (1995) Context-dependent learning in honeybees. *Proc. Austr. Neurosci. Soc.* 6: 226.

Gamlin, P. D. R., Reiner, A., Keyer, K. T., Brecha, N., and Karten, H. J. (1996) Projection of the nucleus pretectalis to a retino-recipient tectal layer in the pigeon (Columba livia). *J. Comp. Neurol.* 368: 424–438.

Ganihar, D., Libersat, F., Wendler, G., and Camhi, J. M. (1994) Wind-evoked escape responses in flying cockroaches. *J. Comp. Physiol.* 175: 49–65.

Gans, C. (1961) A bullfrog and its prey. *Nat. Hist.* 70: 26–37.

Gardenfors, P. (1996) Cued and detached representations in animal cognition. *Behav. Proc.* 35: 263–273.

Gaze, R. M. (1958) The representation of the retina on the optic lobe of the frog. *Quart. J. Exp. Physiol.* 43: 209–314.

Gebhardt, M. and Honegger, H.-W. (2001) Physiological characterization of antennal mechanosensory descending interneurons in an insect (*Gryllus bimaculatus*, *Gryllus campestris*) brain. *J. Exp. Biol.* 204: 2265–2275.

Gegear, R. J. and Laverty, T. M. (2001) The effect of variation among floral traits on the flower constancy of pollinators. In L. Chittka and J. D. Thomson (eds.), *Cognitive Ecology of Pollination*. Cambridge: Cambridge Univ. Press, pp. 1–20.

Gerhardt, H. C. and Huber, F. (2002) *Acoustic Communication in Insects and Anurans: Common Problems and Diverse Solutions*. Chicago: University of Chicago Press.

Gewecke, M. and Hou, T. (1993) Visual brain neurons in *Locusta migratoria*. In K. Weise, F. G. Gribakin, A. V. Popov, and G. Renninger (eds.), *Sensory Systems in Arthropods*. Basel Switzerland: Birkhäuser, pp. 119–144.

Gillespie, P. G. and Walker, R. G. (2001) Molecular basis of mechanosensory transduction. *Nature* 413: 194–202.

Giurfa, M. and Lehrer, M. (2001) Honeybee vision and floral displays: From detection to close-up recognition. In L. Chittka and J. D. Thomson (eds.), *Cognitive Ecology of Pollination*. Cambridge: Cambridge Univ. Press, pp. 61–82.

Giurfa, M., Núñez, J., Chittka, L., and Menzel, R. (1995) Colour preferences of flower-naive honeybees. *J. Comp. Physiol. A* 177: 247–259.

Giurfa, M., Eichmann, B., and Menzel, R. (1996) Symmetry perception in an insect. *Nature* 382: 458–461.

Giurfa, M., Zhang, S. W., Jenett, A., Menzel, R., and Srinivasan, M. V. (2001) The concepts of "sameness" and "difference" in an insect. *Nature* 410: 930–933.

Glantz, R. M. (2001) Polarization analysis in the crayfish visual system. *J. Exp. Biol.* 204: 2383–2390.

Gleadall, I. G. (1994) A model for enhancing the visual information available under low light conditions. *Interdis. Infor. Sci.* 1: 67–75.

Gleadall, I. G., Ohtsu, K., Gleadall, E., and Tsukahara, Y. (1993) Screening-pigment migration in the octopus retina includes control by dopaminergic efferents. *J. Exp. Biol.* 185: 1–16.

Gnatzy, W. and Heusslein, R. (1986) Digger wasp against cricket. *Naturwissenschaften* 73: 212–215.

Gnatzy, W. and Kamper, G. (1990) Digger wasp against crickets. II. An airborne signal produced by a running predator. *J. Comp. Physiol.* 167: 551–556.

Gogala, M. and Riede, K. (1995) Time sharing of song activity by cicadas in Temengor Forest Reserve, Hulu Perak and in Sabah, Malaysia. *Malay. Nat. J.* 49: 48–54.

Goldman, M., Lanson, R., and Rivera, G. (1991) Wavelength categorization by goldfish (*Carassius auratus*). *Int. J. Comp. Psychol.* 4: 195–210.

Goldsmith, T. H. (1978) The effects of screening pigments on the spectral sensitivity of some Crustacea with scotopic (superposition) eyes. *Vision Res.* 18: 475–482.

Goldsmith, T. H. (1990) Optimization, constraint and history in the evolution of eyes. *Quart. Rev. Biol.* 65: 281–322.

Goldsmith, T. H. (1991) *Photoreception and Vision*. New York: Wiley-Liss.

Goldsmith, T. H. (1994) Ultraviolet receptors and color vision: Evolutionary implications and a dissonance of paradigms. *Vision Res.* 34: 1479–1487.

Goldsmith, T. H. and Fernandez, H. R. (1968) Comparative studies of crustacean spectral sensitivity. *Z. Verg. Physiol.* 60: 156–175.

Goldsmith, T. H. and Wehner, R. (1977) Restrictions on rotational and translational diffusion of pigment in the membranes of a rhabdomeric photoreceptor. *J. Gen. Physiol.* 70: 453–490.

Goldstein, E. B. (1989) *Sensation and Perception*. Belmont, Calif.: Wadsworth.

Gombocz, M. (1999) Verhaltensbeobachtungen an der Gottesanbeterin *Empusa fasciata* in ihrer natürlichen Umgebung. Master's thesis, Univ. of Graz, Graz, Austria.

Gonka, M. D., Laurie, T. J., and Prete, F. R. (1999) Responses of movement-sensitive descending visual interneurons to prey-like stimuli in the praying mantis, *Sphodromantis lineola* (Burmeister). *Brain, Behav., Evol.* 54: 243–262.

Gorochov, A. V. (1995) Contribution to the system and evolution of the order Orthoptera. *Zool. Zhur.* 74: 39–45.

Gould, J. L. and Gould, C. G. (1988) *The Sensory World in the Honey Bee*. New York: Scientific American Library, pp. 41–45.

Govardovskii, V. I. (1983) On the role of oil drops in colour vision. *Vision Res.* 23: 1739–1740.

Gras, H. and Horner, M. (1992) Wind-evoked escape running of the cricket *Gryllus bimaculatus*. I. Behavioral analysis. *J. Exp. Biol.* 171: 189–214.

Gray, L. A., O'Reilly, J. C., and Nishikawa, K. C. (1997) Evolution of forelimb movement patterns for prey manipulation in anurans. *J. Exp. Zool.* 277: 417–424.

Graziadei, P. (1962) Receptors in the suckers of the octopus. *Nature (London)* 195: 57–59.

Graziadei, P. (1964) Receptors in the sucker of the cuttlefish. *Nature (London)* 203: 384–386.

Graziadei, P. (1971) The nervous system of the arms. In J. Z. Young (ed.), *The Anatomy of the Nervous System of Octopus vulgaris*. Oxford: Oxford Univ. Press, pp. 45–61.

Graziadei, P. and Gagne, H. T. (1976a) Sensory innervation in the rim of the octopus sucker. *J. Morphol.* 150: 639–680.

Graziadei, P. and Gagne, H. T. (1976b) An unusual receptor in the octopus. *Cell Tiss. Res.* 8: 229–240.

Greenfield, M. D. (1988) Interspecific acoustic interactions among katydids' *neoconocephalus*-inhibition-induced shifts in diel periodicity. *Anim. Behav.* 36: 684–695.

Greenfield, M. D. (2002) *Signalers and Receivers: Mechanisms and Evolution of Arthropod Communication*. Oxford: Oxford Univ. Press.

Gribakin, F. C. (1975) Functional morphology of the compound eye of the bee. In G. A. Horridge (ed.), *The Compound Eye and Vision of Insects*. Oxford: Clarendon Press, pp. 154–176.

Grobstein, P. (1991) Directed movement in the frog: A closer look at a central representation of spatial location. In M. A. Arbib and J.-P. Ewert (eds.), *Visual Structures and Integrated Functions*. Berlin: Springer-Verlag, pp. 125–138.

Grobstein, P., Comer, C. and Kostyk, S. K. (1983) Frog prey capture behavior: Between sensory maps and directed motor output. In J.-P. Ewert, R. R. Capranica, and D. J. Ingle (eds.), *Advances in Vertebrate Neuroethology*. New York: Plenum, pp. 331–347.

Gruberg, E. R. and Ambros, V. R. (1974) A forebrain visual projection in the frog (*Rana pipiens*). *Exp. Brain Res.* 44: 187–197.

Grüsser, O.-J. and Grüsser-Cornehls, U. (1976) Neurophysiology of the anuran visual system. In R. Llinás and W. Precht (eds.), *Frog Neurobiology*. Berlin: Springer-Verlag, pp. 297–385.

Grüsser, O.-J., Grüsser-Cornehls, U., Finkelstein, D., Henn, V., Patutschnik, M., and Butenandt, E. (1967) A quantitative analysis of movement-detecting neurons in the frog retina. *Pflügers Arch.* 293: 100–106.

Guha, K., Jørgensen, C. B., and Larsen, L. O. (1980) Relationship between nutritional state and testes function, together with the observations on patterns of feeding, in the toad. *J. Zool. (Lond.)* 192: 147–155.

Gumbert, A. (2000) Color choices by bumble bees (*Bombus terrestris*): Innate preferences and generalization after learning. *Behav. Ecol. Sociobiol.* 48: 36–43.

Hafner, G. S. and Tokarski, T. R. (1998) Morphogenesis and pattern formation in the retina of the crayfish *Procambarus clarkii*. *Cell Tiss. Res.* 293: 535–550.

Hamacher, K. and Stieve, H. (1984) Spectral properties of the rhodopsin of the crayfish *Astacus leptodactylus*. *Photochem. Photobiol.* 39: 379–390.

Hamanaka, T., Kito, Y., Seidou, M., Wakabayashi, K., Michinomae, M., and Amemiya, Y. (1994) X-ray diffraction study of the live squid retina. *J. Mol. Biol.* 238: 139–144.

Hamasaki, D. I. (1968a) The electororetinogram of the intact anesthetized octopus. *Vision Res.* 8: 247–258.

Hamasaki, D. I. (1968b) The ERG-determined spectral sensitivity of the octopus. *Vision Res.* 8: 1013–1021.

Hamdorf, K., Schwemer, J., and Tauber, U. (1968) The visual pigment, the absorption of the photoreceptors and the spectral sensitivity of the retina of *Eledone moschata*. *Z. Vergl. Physiol.* 60: 375–415.

Hamilton, W. D. (1979) Wingless and fighting males in fig wasps and other insects. In M. S. Blum and N. A. Blum (eds.), *Sexual Selection and Reproductive Competition in Insects*. New York: Academic Press, pp. 167–220.

Hammer, M. and Menzel, R. (1995) Learning and memory in the honeybee. *J. Neurosci.* 15(3): 1617–1630.

Hanlon, R. T. and Messenger, J. B. (1988) Adaptive coloration in young cuttlefish (*Sepia officinalis* L.): The morphology and development of body patterns and their relation to behaviour. *Phil. Trans. Roy. Soc. Lond.* 320: 437–487.

Hanlon, R. T. and Messenger, J. B. (1996) *Cephalopod Behaviour*. Cambridge: Cambridge Univ. Press.

Hanlon, R. T. and Shashar, N. (2003) Aspects of the sensory ecology of cephalopods. In S. P. Collin and J. Marshall (eds.), *Sensory Processing of the Aquatic Environment*. New York: Springer-Verlag.

Hanlon, R. T., Forsythe, J. W., and Joneschild, D. E. (1999a) Crypsis, conspicuousness, mimicry and polyphenism as antipredator defences of foraging octopuses on Indo-Pacific coral reefs, with a method of quantifying crypsis from video tapes. *Biol. J. Linn. Soc.* 66: 1–22.

Hanlon, R. T., Maxwell, M. R., Shashar, N., Loew, E. R., and Boyle, K. L. (1999b) An ethogram of body patterning behavior in the biomedically and commercially valuable squid *Loligo pealei* off Cape Cod, Massachusetts. *Biol. Bull.* 197: 49–62.

Hansen-Delkeskamp, E. (1992) Functional characterization of antennal contact chemoreceptors in the cockroach *Periplaneta americana*. An electrophysiological investigation. *J. Insect Physiol.* 38: 813–822.

Hardie, R. C. (1986) The photoreceptor array of the dipteran retina. *Trends Neurosci.* 9: 419–423.

Hardie, R. C. and Duelli, P. (1978) Properties of single cells in posterior lateral eyes of jumping spiders. *Z. Naturforsch.* 33c: 156–158.

Hardie, R. C., Franceschini, N., Ribi, W., and Kirschfeld, K. (1981) Distribution and properties of sex-specific photoreceptors in the fly *Musca domestica*. *J. Comp. Physiol. A* 145: 139–152.

Hariyama, T. and Tsukahara, Y. (1988) Seasonal variation of spectral sensitivity in crayfish retinula cells. *Comp. Biochem. Physiol.* 91A(3): 529–533.

Hariyama, T., Gleadall, I. G., Liao, L., Gleadall, E., and Tsukahara, Y. (1989) Details of the production of monoclonal antibodies to demonstrate the presence (in winter) of more than one type of opsin in the retinula cells of the crayfish, *Procambarus clarkii* Girard. *Ann. App. Inform. Sci.* 14(2): 101–113.

Harland, D. P. and Jackson, R. R. (2000a) Cues by which *Portia fimbriata*, an araneophagic jumping spider, distinguishes jumping-spider prey from other prey. *J. Exp. Biol.* 203: 3485–3494.

Harland, D. P. and Jackson, R. R. (2000b) “Eight-legged cats” and how they see—a review of recent work on jumping spiders (Araneae: Salticidae). *Cimbebasia* 16: 231–240.

Harland, D. P. and Jackson, R. R. (2001) Prey classification by *Portia fimbriata*, a salticid spider that specializes at preying on other salticids: Species that elicit cryptic stalking. *J. Zool. Lond.* 255: 445–460.

Harland, D. P. and Jackson, R. R. (2002) Influence of cues from the anterior medial eyes of virtual prey on *Portia fimbriata*, an araneophagic jumping spider. *J. Exp. Biol.* 205: 1861–1868.

Harland, D. P., Jackson, R. R., and Macnab, A. (1999) Distances at which jumping spiders (Araneae, Salticidae) distinguish between prey and conspecific rivals. *J. Zool. Lond.* 247: 357–364.

Harling, C. (2000) Re-examination of eye design in the classification of stomatopod crustaceans. *J. Crust. Biol.* 20: 172–185.

Harwood, D. V. and Anderson, C. W. (2000) Evidence for the anatomical origins of hypoglossal afferents in the tongue of the leopard frog, *Rana pipiens*. *Brain Res.* 862: 288–291.

Hawryshyn, C. W. (1992) Polarization vision in fish. *Am. Sci.* 80: 164–175.

Heide, G., Berger, F., and Mebus, U. (1982) Neurale und neuromuskuläre Korrelate des visuell auslösbaren Kopfstellreflexes bei *Mantis religiosa*. *Verh. Dtsch. Zool. Ges.* 274.

Heider, E. R. and Olivier, D. C. (1972) The structure of the color space in naming and memory for two languages. *Cog. Psychol.* 3: 337–354.

Heil, K. H. (1936) Beiträge zur Physiologie und Psychologie der Springspinnen. *Z. Vergl. Phsyiol.* 23: 125–149.

Heinrich, B. (1979) *Bumblebee Economics*. Cambridge, Mass.: Harvard Univ. Press.

Heinrich, B., Mudge P. R., and Deringis P. G. (1977) Laboratory analysis of flower constancy in foraging bumblebees: *Bombus ternarius* and *B. terricola*. *Behav. Ecol. Sociobiol.* 2: 247–265.

Hemmi, J. M. (1999) Dichromatic colour vision in an Australian marsupial, the tammar wallaby. *J. Comp. Physiol. A* 185: 509–515.

Hempel, de Ibarra, N., Giurfa, M., and Vorobyev, M. (2001) Detection of coloured patterns by honeybees through chromatic and achromatic cues. *J. Comp. Physiol. A* 187: 215–224.

Herman, L. M. and Gordon, J. A. (1974) Auditory delayed matching in the bottlenose dolphin. *J. Exp. Anal. Behav.* 21: 19–26.

Herrick, C. J. (1933) The amphibian forebrain. VIII: Cerebral hemispheres and pallial primordia. *J. Comp. Neurol.* 58: 737–759.

Hertel, H. (1980) Chromatic properties of identified interneurons in the optic lobes of the bee. *J. Comp. Physiol.* 137: 215–231.

Hertel, H. and Maronde, U. (1987a) Processing of visual information in the honeybee brain. In R. Menzel and A. Mercer (eds.), *Neurobiology and Behavior of Honeybees*, Berlin: Springer-Verlag, pp. 141–157.

Hertel, H. and Maronde, U. (1987b) The physiology and morphology of centrally projecting visual interneurones in the honeybee brain. *J. Exp. Biol.* 133: 301–315.

Hill, D. E. (1979) Orientation by jumping spiders of the genus *Phidippus* (Araneae: Salticidae) during the pursuit of prey. *Behav. Ecol. Sociobiol.* 5: 301–322.

Hill, P. S. M., Wells, P. H., and Wells, H. (1997) Spontaneous flower constancy and learning in honey bees as a function of colour. *Anim. Behav.* 54: 615–627.

Hill, P. S. M., Hollis, J., and Wells, H. (2001) Foraging decisions in nectarivores: Unexpected interactions between flower constancy and energetic rewards. *Anim. Behav.* 62: 729–737.

Himstedt, W. (1982) Prey selection in salamanders. In D. J. Ingle, M. A. Goodale, and R. J. W. Mansfield (eds.), *Analysis of Visual Behavior*. Cambridge, Mass: MIT Press, pp. 47–66.

Himstedt, W. and Plasa, L. (1979) Home-site orientation by visual cues in salamanders. *Naturwissenschaften* 66: 372–373.

Himstedt, W., Freidank, U., and Singer, E. (1976) Die Veränderung eines Auslösemechanismus im Beutefangverhalten während der Entwicklung von *Salamandra salamandra* (L.). *Z. Tierpsychol.* 41: 235–243.

Himstedt, W., Tempel, R., and Weiler, J. (1978) Responses of salamanders to stationary visual patterns. *J. Comp. Psychol.* 124: 49–52.

Hirota, K., Sonoda, Y., Baba, Y., and Yamaguchi, T. (1993) Distinction in morphology and behavioral role between dorsal and ventral group of cricket giant interneurons. *Zool. Sci.* 10: 705–709.

Holmes, P. W. (1979) Transfer of matching performance in pigeons. *J. Exp. Anal. Behav.* 31: 103–114.

Homann, H. (1928) Beträge zur Physiologie der Spinnenaugen. I. Untersuchungsmethoden, II. Das Sehvermöen der Salticiden. *Z. Vergl. Physiol.* 7: 201–268.

Honegger, H.-W. (1981) A preliminary note on a new optomotor response in crickets: Antennal tracking of moving targets. *J. Comp. Physiol.* 142: 419–421.

Honegger, H.-W., Bartos, M., Gramm, T., and Gebhardt, M. (1995) Peripheral modulation and plasticity of antennal movements in crickets. *Verh. Dtsch. Zool. Ges.* 88.2: 129–137.

Hope, A. J., Partridge, J. C., Dulai, K. S., and Hunt, D. M. (1997) Mechanisms of wavelength tuning in the rod opsins of deep-sea fishes. *Proc. Roy. Soc. Lond. B* 264: 155–163.

Horridge, G. A. (1978) The separation of visual axes in apposition compound eyes. *Phil. Trans. Roy. Soc. Lond. B* 285: 1–59.

Horridge, G. A. (1980) Apposition eyes of large diurnal insects as organs adapted to seeing. *Proc. Roy. Soc. Lond. B* 207: 287–309.

Horridge, G. A. (1996) The honeybee (*Apis mellifera*) detects bilateral symmetry and discriminates its axis. *J. Insect Physiol.* 42(8): 755–764.

Horridge, G. A. (1999) Two-dimensional pattern discrimination by the honeybee. *Physiol. Entomol.* 24: 197–212.

Horridge, G. A. (2000) Seven experiments on pattern vision of the honeybee, with a model. *Vision Res.* 40: 2589–2603.

Horridge, G. A. and Duelli. P. (1979) Anatomy of the regional differences in the eye of the mantis *Ciulfina*. *J. Exp. Biol.* 80: 165–190.

Horridge, G. A. and Zhang, S. W. (1995) Pattern vision in honeybees (*Apis mellifera*): Flower-like patterns with no predominant orientation. *J. Insect Physiol.* 41(8): 681–688.

Horridge, G. A., Zhang, S. W., and O'Carroll, D. (1992a) Insect perception of illusory contours. *Phil. Trans. Roy. Soc. Lond. B* 337: 59–64.

Horridge, G. A., Zhang, S. W., and Lehrer, M. (1992b) Bees can combine range and visual angle to estimate absolute size. *Phil. Trans. Roy. Soc. Lond. B* 337: 49–57.

Horváth, G. and Varjú, D. (1997) Polarization pattern of freshwater habitats recorded by video polarimetry in red, green and blue spectral ranges and its relevance for water detection by aquatic insects. *J. Exp. Biol.* 200: 1155–1163.

Howard, J. (1981) Temporal resolving power of the photoreceptors of *Locusta migratoria*. *J. Comp. Physiol.* 144: 61–66.

Hubel, D. H. and Wiesel T. N. (1962) Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. *J. Physiol.* 160: 106–154.

Huber, F. (1983) Implications of insect neuroethology for studies on vertebrates. In J.-P. Ewert, R. R. Capranica, and D. J. Ingle (eds.), *Advances in Vertebrate Neuroethology*. New York: Plenum, pp. 91–138.

Huber, R. and Delago, A. (1998) Serotonin alters decisions to withdraw in fighting crayfish, *Astacus astacus*: The motivational concept revisited. *J. Comp. Physiol. A* 182: 573–583.

Hurd, L. E. and Eisenberg, R. M. (1984a) Experimental density manipulations of the predator *Tenodera sinensis* (Orthoptera: Mantidae) in an old-field community. I. Mortality, development and dispersal of juvenile mantids. *J. Anim. Ecol.* 53: 269–281.

Hurd, L. E. and Eisenberg, R. M. (1984b) Experimental density manipulations of the predator *Tenodera sinensis* (Orthoptera: Mantidae) in an old-field community. II. The influence of mantids on arthropod community structure. *J. Anim. Ecol.* 53: 955–967.

Hurd, L. E. and Eisenberg, R. M. (1990) Arthropod community responses to manipulation of a bitrophic predator guild. *Ecology* 76: 2107–2114.

Hustert, R. (1978) Segmental and intreganglionic projections from primary fibres of insect mechanoreceptors. *Cell Tiss. Res.* 194: 337–351.

Ibbotson, M. R., Maddess, T., and DuBois, R. (1991) A system of insect neurons sensitive to horizontal and vertical image motion connects the medulla and midbrain. *J. Comp. Physiol. A* 169: 355–367.

Ilse, D. and Vaidya, V. G. (1955) Spontaneous feeding response to colours in *Papilio demoleus* L. *Proc. Ind. Acad. Sci.* 43: 23–31.

Ingle, D. J. (1970) Visuomotor functions of the frog optic tectum. *Brain, Behav. Evol.* 3: 57–71.

Ingle, D. J. (1971) Prey-catching behavior of anurans toward moving and stationary objects. *Vision Res. Suppl.* 3: 447–456.

Ingle, D. J. (1972) Depth vision in monocular frogs. *Psychon. Sci.* 29: 37–38.

Ingle, D. J. (1976a) Spatial vision in anurans. In K. V. Fite (ed.), *The Amphibian Visual System: A Multidisciplinary Approach*. New York: Academic Press, pp. 119–140.

Ingle, D. J. (1976b) Behavioral correlates of central visual function in anurans. In R. Llinás and W. Precht (eds.), *Frog Neurobiology*. Berlin: Springer-Verlag, pp. 435–451.

Ingle, D. J. (1977) Detection of stationary objects by frogs (*Rana pipiens*) after ablation of optic tectum. *J. Comp. Physiol. Psychol.* 91: 1359–1364.

Ingle, D. J. (1979) Effect of pretectum ablation on detection of barriers and apertures by frogs. *Soc. Neurosci. Abstr.* 5: 790.

Ingle, D. J. (1982) Organization of visuomotor behaviors in vertebrates. In D. J. Ingle, M. A. Goodale, and R. J. W. Mansfield (eds.), *Analysis of Visual Behavior*. Cambridge, Mass.: MIT Press, pp. 67–109.

Ingle, D. J. and Cook, J. (1977) The effect of viewing distance upon size preference of frogs for prey. *Vision Res.* 17: 1009–1013.

Ingle, D. J. and McKinley, D. (1978) Effects of stimulus configuration on elicited prey catching by the marine toad (*Bufo marinus*). *Anim. Behav.* 26: 885–891.

Irwin, R. E. and Brody, A. K. (1999) Nectar-robbing bumble bees reduce the fitness of *Ipomopsis aggregata* (Polemoniaceae). *Ecology* 80: 1703–1712.

Ishii S., Kubokawa, K., Kikuchi, M., and Nishio, H. (1995) Orientation of the toad, *Bufo japanicus*, toward the breeding pond. *Zool. Sci.* 12: 475–484.

Ivanoff, A. and Waterman, T. H. (1958) Factors, mainly depth and wavelength, affecting the degree of underwater light polarization. *J. Mar. Res.* 16: 283–307.

Jackson, R. R. (1988) The biology of *Jacksonoides queenslandica*, a jumping spider (Araneae: Salticidae) from Queensland: Intraspecific interactions, web-invasion, predators, and prey. *NZ J. Zool.* 15: 1–37.

Jackson, R. R. (1992) Predator-prey interactions between web-invading jumping spiders and *Argiope appensa* (Araneae, Araneidae), a tropical orb-weaving spider. *J. Zool. Lond.* 228: 509–520.

Jackson, R. R. (1995) Cues for web invasion and aggressive mimicry signalling in *Portia* (Araneae, Salticidae). *J. Zool. Lond.* 236: 131–149.

Jackson, R. R. and Blest, A. D. (1982a) The biology of *Portia fimbriata*, a web-building jumping spider (Araneae, Salticidae) from Queensland: Utilization of webs and predatory versatility. *J. Zool. Lond.* 196: 255–293.

Jackson, R. R. and Blest, A. D. (1982b) The distances at which a primitive jumping spider, *Portia fimbriata*, makes visual discriminations. *J. Exp. Biol.* 97: 441–445.

Jackson, R. R. and Hallas, S. E. A. (1986a) Comparative biology of *Portia africana*, *P. albimana*, *P. fimbriata*, *P. labiata* and *P. schultzi*, araneophagic web-building jumping spiders (Araneae: Salticidae): Utilization of silk, predatory versatility and intraspecific interactions. *NZ J. Zool.* 13: 423–489.

Jackson, R. R. and Hallas, S. E. A. (1986b) Capture efficiencies of web-building jumping spiders (Araneae, Salticidae): Is the jack-of-all-trades the master of none? *J. Zool. Lond.* 209: 1–7.

Jackson, R. R. and Pollard, S. D. (1996) Predatory behavior of jumping spiders. *Ann. Rev. Entomol.* 41: 287–308.

Jackson, R. R. and Wilcox, R. S. (1993a) Spider flexibly chooses aggressive mimicry signals for different prey by trial and error. *Behavior* 127: 21–36.

Jackson, R. R. and Wilcox, R. S. (1993b) Observations in nature of detouring behaviour by *Portia fimbriata*, a web-invading aggressive-mimic jumping spider from Queensland. *J. Zool. Lond.* 230: 135–139.

Jackson, R. R. and Wilcox, R. S. (1998) Spider-eating spiders. *Am. Sci.* 86: 350–357.

Jackson, R. R., Rowe, R. J., and Wilcox, R. S. (1993) Anti-predator defences of *Argiope appensa* (Araneae, Araneidae), a tropical orb-weaving spider. *J. Zool. Lond.* 229: 121–132.

Jackson, R. R., Li, D., Fijn, N., and Barrion, A. (1998) Predatory-prey interactions between aggressive-mimic jumping spiders (Salticidae) and araeneophagic spitting spiders (Scytodidae) from the Philippines. *J. Insect. Behav.* 11: 319–342.

Jackson, R. R., Carter, C. M., and Tarsitano, M. S. (2001) Trial-and-error solving of a confinement problem by a jumping spider, *Portia fimbriata*. *Behavior* 138: 1215–1234.

Jackson, R. R., Clark, R. J., and Harland, D. P. (2002) Behavioural and cognitive influences of kairomones from *Jacksonoides queenslandicus* (Araneae, Salticidae) on *Portia fimbriata*, an araneophagic salticid spider that specializes at preying on other salticids. *Behavior* 139: 749–775.

Jacobs, G. A. and Murphey, R. K. (1987) Segmental origins of the cricket giant interneuron system. *J. Comp. Neurol.* 265: 145–157.

Jacobs, G. A. and Theunissen, F. E. (1996) Functional organization of a neural map in the cricket cercal sensory system. *J. Neurosci.* 16: 769–784.

Jacobs, G. H. (1993) The distribution and nature of colour vision among the mammals. *Biol. Rev. Camb. Phil. Soc.* 68: 413–471.

Jacobs, K., Otte, B., and Lakes-Harlan, R. (1999) Tympanal receptor cells of *Schistocera gregaria*: Correlation of soma positions and dendrite attachment sites, central projections and physiologies. *J. Exp. Zool.* 283: 270–285.

James, A. C. and Osorio, D. (1996) Characterisation of columnar neurons and visual signal processing in the medulla of the locust optic lobe by system identification techniques. *J. Comp. Physiol. A* 178: 183–199.

Jander, R., Daumer, K., and Waterman, T. H. (1963) Polarized light orientation by two Hawaiian decapod cephalopods. *Z. Vergl. Physiol.* 46: 383–394.

Jander, U. and Jander, R. (2002) Allometry and resolution of bee eyes (Apoidea). *Arth. Struct. Dev.* 30: 179–193.

Jenkins, F. A. and White, H. E. (1976) *Fundamentals of Optics*. Tokyo: McGraw-Hill Kogakusha.

Jerison, H. J. (1973) *Evolution of the Brain and Intelligence*. New York: Academic Press.

Jerison, H. J. (1985) On the evolution of mind. In D. A. Oackley (ed.), *Brain and Mind, Psychology in Progress*. London, New York: Methuen, pp. 1–31.

Johnson, M. D. (1976) Concerning the feeding habits of the praying mantis *Tenodera aridifolia sinensis*, Saussure. *J. Kansas Ent. Soc.* 49: 164.

Judd, S. P. D. and Collett, T. S. (1998) Multiple stored views and landmark guidance in ants. *Nature* 392 (6677): 710–714.

Judge, S. J. and Rind, F. C. (1997) The locust DCMD, a movement-detecting neurone tightly tuned to collision trajectories. *J. Exp. Biol.* 200: 2209–2216.

Julesz, B. (1971) *The Foundations of Cyclopean Perception*. Chicago: Univ. of Chicago Press.

Kaiser, W. (1974) The spectral sensitivity of the honeybee optomotor walking response. *J. Comp. Physiol.* 90: 405–408.

Kaiser, W. and Seidl, R. (1977) The participation of all three colour receptors in the phototactic behaviour of fixed walking honeybees. *J. Comp. Physiol.* 122: 27–44.

Kamil, A. C. (1998) On the proper definition of cognitive ethology. In I. M. Pepperberg, A. Kamil, and R. Balda (eds.), *Animal Cognition in Nature*. New York: Academic Press, pp. 1–28.

Kandori, I. and Ohsaki, N. (1996) The learning abilities of the white cabbage butterfly, *Pieris rapae*, foraging for flowers. *Res. Popul. Ecol.* 38: 111–117.

Kaps, F. and Schmid, A. (1996) Mechanisms and possible behavioural relevance of retinal movements in the ctenid spider *Cupiennius salei*. *J. Exp. Biol.* 199: 2451–2458.

Kästner, A. (1950) Reaktionen der Hüpfspinnen (Salticidae) auf unbewegte farblose und farbige Gesichtsreize. *Zool. Beitr.* 1: 13–50.

Katte, O. and Hoffmann, K.-P. (1980) Direction specific neurons in the pretectum of the frog (*Rana esculenta*). *J. Comp. Physiol.* 140: 53–57.

Kawahara, M., Gleadall, I. G., and Tsukahara, Y. (1998) A note on the fibre-optic light-guides in the eye photophores of *Watasenia scintillans*. *S. Afr. J. Mar. Sci.* 20: 123–127.

Kay, P. and McDaniel, C. K. (1978) The linguistic significance of the meanings of basic color terms. *Language* 54: 610–646.

Kelber, A. (1997) Innate preferences for flower features in the hawkmoth *Macroglossum stellatarum*. *J. Exp. Biol.* 200: 827–836.

Kelber, A. (1999a) Ovipositing butterflies use a red receptor to see green. *J. Exp. Biol.* 202: 2619–2630.

Kelber, A. (1999b) Why “false” colours are seen by butterflies. *Nature* 402: 251.

Kelber, A. and Henique, U. (1999) Trichromatic colour vision in the hummingbird hawkmoth, *Macroglossum stellatarum* L. *J. Comp. Physiol. A* 184: 535–541.

Kelber, A. and Pfaff, M. (1999) True colour vision in the orchard butterfly, *Papilio aegeus*. *Naturwissenschaften* 86: 221–224.

Kelber, A., Thunell, C., and Arikawa, K. (2001) Polarisation-dependent colour vision in *Papilio* butterflies. *J. Exp. Biol.* 204: 2469–2480.

Kennedy, D. and Bruno, M. S. (1961) The spectral sensitivity of crayfish and lobster vision. *J. Gen. Physiol.* 44: 1089–1102.

Kennedy, J. S. (1945) Observations on the mass migration of desert locust hoppers. *Trans. Roy. Entomol. Soc. Lond.* 95: 247–262.

Keskinen, E., Takaku, Y., Meyer-Rochow, V. B., and Hariyama, T. (2002) Postembryonic eye growth in the seashore Isopod *Ligia exotica* (Crustacea, Isopoda) *Biol. Bull.* 202: 223–231.

Kevan, P. G., Chittka, L., and Dyer, A. G. (2001) Limits to the salience of ultraviolet: Lessons from colour vision in bees and birds. *J. Exp. Biol.* 204: 2571–2580.

Kicliter, E. (1973) Flux, wavelength and movement discrimination in the frogs: Forebrain and midbrain contributions. *Brain. Behav. Evol.* 8: 340–365.

Kicliter, E. and Goytia, E. J. (1995) A comparison of spectral response functions of positive and negative phototaxis in two anuran amphibians, *Rana pipiens* and *Leptodactylus pentadactylus*. *Neurosci. Lett.* 185: 144–146.

Kien, J. and Menzel, R. (1977a) Chromatic properties of interneurons in the optic lobes of the bee. I.Broad band neurons. *J. Comp. Physiol.* 113: 17–34.

Kien, J. and Menzel, R. (1977b) Chromatic properties of interneurons in the optic lobes of the bee. II. Narrow band and colour opponent neurons. *J. Comp. Physiol. A* 113: 35–53.

King-Leung, K. and Goldsmith, T. H. (1977) Photosensitivity of retinular cells in white-eyed crayfish (*Procambarus clarkii*). *J. Comp. Physiol. A* 122: 273–288.

Kinoshita, M. and Arikawa, K. (2000) Colour constancy of the swallowtail butterfly, *Papilio xuthus*. *J. Exp. Biol.* 203: 3521–3530.

Kinoshita M., Sato, M., and Arikawa, K. (1997) Spectral receptors of nymphalid butterflies. *Naturwissenschaften* 84: 199–201.

Kinoshita, M., Shimada, N., and Arikawa, K. (1999) Colour vision of the foraging swallowtail butterfly *Papilio xuthus*. *J. Exp. Biol.* 202: 95–102.

Kirschfeld, K. (1976) The resolution of lens and compound eyes. In F. Zettler and R. Weiler (eds.), *Neural Principles in Vision*. Berlin: Springer-Verlag, pp. 354–370.

Kitamoto, J., Sakamoto, K., Ozaki, K., Mishina, Y., and Arikawa, K. (1998) Two visual pigments in a single photoreceptor cell: Identification and histological localization of three mRNAs encoding visual pigment opsins in the retina of the butterfly *Papilio xuthus*. *J. Exp. Biol.* 201: 1255–1261.

Kitamoto, J., Ozaki, K., and Arikawa, K. (2000) Ultraviolet and violet receptors express identical mRNA encoding an ultraviolet-absorbing opsin: Identification and histological localization of two mRNAs encoding short-wavelength-absorbing opsins in the retina of the butterfly *Papilio xuthus*. *J. Exp. Biol.* 203: 2887–2894.

Knowles, A. and Dartnall, H. J. A. (1977) Habitat and visual pigments. In H. Davson (ed.), *The Eye*. vol. 2B, *The Photobiology of Vision*. New York: Academic Press, pp. 581–641.

Kolb, G. (1986) Retinal ultrastructure in the dorsal rim and large dorsal area of the eye of *Aglais urticae* (Lepidoptera). *Zoomorphology* 106: 244–246.

Kolb, G. and Scherer, C. (1982) Experiments on wavelength specific behavior of *Pieris brassicae* L. during drumming and egg-laying. *J. Comp. Physiol. A* 149: 325–332.

Kolton, L. and Camhi, J. M. (1995) Cartesian representation of stimulus direction: Parallel processing by two sets of giant interneurons in the cockroach. *J. Comp. Physiol.* 176: 691–702.

Kondrashev, S. L. (1987) Neuroethology and color vision in amphibians. *Behav. Brain Sci.* 10: 385.

Kong, K. L., Fung, Y. M., and Wasserman, G. S. (1980) Filter-mediated color vision with one visual pigment. *Science* 207: 783–786.

Kozicz, T. and Lázár, G. (1994) The origin of tectal NPY immunopositive fibers in the frog. *Brain Res.* 635: 345–348.

Kozicz, T. and Lázár, G. (2001) Colocalization of GABA, enkephalin and neuropeptide Y in the tectum of the green frog *Rana esculenta*. *Peptides* 22: 1071–1077.

Kral, K. (1987) Organization of the first optic neuropile (or lamina) in different insect species. In A. P. Gupta (ed.), The *Arthropod Brain: Its Evolution, Development, Structure and Functions*. New York: Wiley, pp. 181–201.

Kral, K. (1998a) Side-to-side movements to obtain motion depth cues: A short review of research on the praying mantis. *Behav. Proc.* 43: 71–77.

Kral, K. (1998b) Spatial vision in the course of an insect's life. *Brain Behav. Evol.* 52: 1–6.

Kral, K. (1999) Binocular vision and distance estimation. In F. R. Prete, H. Wells, P. Wells, and L. E. Hurd (eds.), *The Praying Mantids*. Baltimore, Md.: Johns Hopkins Univ. Press, pp. 114–140.

Kral, K. and Devetak, D. (1999) The visual orientation strategies of *Mantis religiosa* and *Empusa fasciata* reflect differences in the structure of their visual surroundings. *J. Insect Behav.* 12: 737–752.

Kral, K. and Poteser, M. (1997) Motion parallax as a source of distance information in locusts and mantids. *J. Insect Behav.* 10: 145–163.

Krebs, W. and Lietz, R. (1982) Apical region of the crayfish retinula. *Cell Tiss. Res.* 222: 409–415.

Kretz, R. (1979) A behavioural analysis of colour vision in the ant *Cataglyphis bicolor* (Formicidae, Hymenoptera). *J. Comp. Physiol. A* 131: 217–233.

Kriska, G., Horvath, G., and Andrikovics, S. (1998) Why do mayflies lay their eggs en masse on dry asphalt roads? Water-imitating polarized light reflected from asphalt attracts Ephemeroptera. *J. Exp. Biol.* 201: 2273–2286.

Kristensen, N. P. (1991) Phylogeny of extant hexapods. In I. D. Naumann, P. B. Carne, J. F. Lawrence, E. S. Nielsen, J. P. Spradbery, R. W. Taylor, M. J. Whitten, and M. J. Littlejohn (eds.), *The Insects of Australia: A Textbook for Students and Research Workers*. Melbourne: CSIRO, Melbourne University Press, pp. 125–140.

Krout, K. E., Loewy, A. D., Westby, G. W. M., and Redgrave, P. (2001) Superior colliculus projections to midline and intralaminar thalamic nuclei of the rat. *J. Comp. Neurol.* 431: 198–216.

Kühn, A. (1924) Versuche über das Unterscheidungsvermögen der Bienen und Fische für Spektrallichter. *Nachr. D. Ges. Wiss.* 1: 66–71.

Kunze, J. and Gumbert, A. (2001) The combined effect of color and odor on flower choice behavior of bumble bees in flower mimicry systems. *Behav. Ecol.* 12: 447–456.

Kunze, P. and Boschek, C. B. (1968) Elektronmikroskopische Untersuchung zur Form der achten Retinulazelle bei Ocypode. *Z. Naturforsch.* 23: 568–569.

Kupfermann, I. and Weiss, K. R. (1978) The command neuron concept. *Behav. Brain Sci.* 1: 3–39.

Kurasawa, M., Wakakuwa, M., Kitamoto, J., Giurfa, M., and Arikawa, K. (2002) Spectral heterogeneity of the ommatidia in the retina of worker honeybees: A molecular phylogenetic study demonstrating three types of ommatidia. *Proc. XIV Int. Meeting IUSSI*, Sapporo, Japan. Sapporo, Japan: Hokkaido University, p. 72.

Labhart, T. and Nilsson, D. E. (1995) The dorsal eye of the dragonfly Sympetrum: Specializations for prey detection against the sky. *J. Comp. Physiol. A* 176: 437–453.

Lam, D. M. K., Wiesel, T. N., and Kaneko, A. (1974) Neurotransmitter synthesis in cephalopod retina. *Brain Res.* 82: 365–368.

Laming, P. R. and Cairns, C. (1998) Effects of food, glucose and water ingestion on feeding activity in the toad (*Bufo bufo*). *Behav. Neurosci.* 112: 1266–1272.

Land, E. H. (1977) The retinex theory of color vision. *Sci. Am.* 237: 108–128.

Land, M. F. (1969a) Structure of the retinae of the eyes of jumping spiders (Salticidae: Dendryphantinae) in relation to visual optics. *J. Exp. Biol.* 51: 443–470.

Land, M. F. (1969b) Movements of the retinae of jumping spiders (Salticidae: Dendryphantinae) in response to visual stimuli. *J. Exp. Biol.* 51: 471–493.

Land, M. F. (1971) Orientation by jumping spiders in the absence of visual feedback. *J. Exp. Biol.* 54: 119–139.

Land, M. F. (1972) Stepping movements made by jumping spiders during turns mediated by the lateral eyes. *J. Exp. Biol.* 57: 15–40.

Land, M. F. (1974) A comparison of the visual behaviour of a predatory arthropod with that of a mammal. In C. A. G. Wiersma (ed.), *Invertebrate Neurons and Behavior*. Cambridge, Mass: MIT Press, pp. 411–418.

Land, M. F. (1981) Optics and vision in invertebrates. In H. Autrum (ed.), *Handbook of Sensory Physiology*. vol. VII/6B, *Comparative Physiology and Evolution of Vision in Invertebrates*. Berlin: Springer-Verlag, pp. 471–592.

Land, M. F. (1984) Molluscs. In M. Ali (ed.), *Photoreception and Vision in Invertebrates*. NATO Advanced Science Series A, vol. 74, New York: Plenum, pp. 699–725.

Land, M. F. (1985a) The morphology and optics of spider eyes. In F. G. Barth (ed.), *Neurobiology of Arachnids*. Berlin: Springer-Verlag, pp. 53–78.

Land, M. F. (1985b) Fields of view of the eyes of primitive jumping spiders. *J. Exp. Biol*. 119: 381–384.

Land, M. F. (1993) Old twist in a new tale. *Nature* 363: 581–852.

Land, M. F. (1995) The functions of eye movements in animals remote from man. In J. M. Findlay (ed.), *Eye Movement Research*. Amsterdam: Elsevier, pp. 63–76.

Land, M. F. (1997) Visual acuity in insects. *Annu. Rev. Entomol.* 42: 147–177.

Land, M. F. and Furneaux, S. (1997) The knowledge base of the oculomotor system. *Phil. Trans. Roy. Soc. Lond. B* 352: 1231–1239.

Land, M. F. and Nilsson D. E. (2002) *Animal Eyes*. Oxford: Oxford Univ. Press.

Land, M. F., Marshall, N. J., Brownless, D., and Cronin, T. W. (1990) The eye-movements of the mantis shrimp *Odontodactylus scyllarus* (Crustacea: stomatopods). *J. Comp. Physiol. A* 167: 155–166.

Lange, G. D. and Hartline, P. H. (1974) Retinal responses in squid and octopus. *J. Comp. Physiol*. 93: 19–36.

Lange, G. D., Hartline, P. H., and Hurley, A. C. (1976) The question of lateral interactions in the retinas of cephalopods. In F. Zettler and R. Weiler (eds.), *Neural Principles in Vision*. Berlin: Springer-Verlag, pp. 89–93.

Langley, C. M., Riley, D. A., Bond, A. B. and Goel, N. (1996) Visual search for natural grains in pigeons (*Columba livia*): Search images and selective attention. *J. Exp. Psychol. Anim. Behav. Proc*. 22: 139–151.

Lashley, K. S. (1949) Persistent problems in the evolution of mind. Quart. Rev. Biol. 24: 28–42.

Laughlin, S. B. (1981) Neural principles in the peripheral visual systems of invertebrates. In H. Autrum (ed.), *Handbook of Sensory Physiology*. vol. VII/6B, *Comparative Physiology and Evolution of Vision in Invertebrates*. Berlin: Springer-Verlag, pp. 133–280.

Laughlin, S. B. (1989) Coding efficiency and design in visual processing. In D. G. Stavenga and R. C. Hardie (eds.), *Facets of Vision*. Berlin: Springer-Verlag, pp. 213–234.

Laughlin, S. B., Howard, J., and Blakeslee, B. (1987) Synaptic limitations to contrast coding in the retina of the blowfly *Calliphora*. *Proc. Roy. Soc. Lond. B* 231: 437–467.

Lázár, G. (1971) The projection of the retinal quadrants on the optic centers in the frog: A terminal degeneration study. *Acta Morph. Acad. Sci. Hung.* 19: 325–334.

Lázár, G. (1973) Role of accessory optic system in the optokinetic nystagmus of the frog. *Brain Behav. Evol.* 5: 443–460.

Lázár, G. (1979) Organization of the frog visual system. In K. Lissák (ed.), *Recent Developments of Neurobiology in Hungary*, vol. 8. Budapest: Akadémiai Kiadò, pp. 9–50.

Lázár, G. (1984) Structure and connections of the frog optic tectum. In H. Vanegas (ed.), *Comparative Neurology of the Optic Tectum*. New York: Plenum, pp. 185–210.

Lázár, G. (1989) Cellular architecture and connectivity of the frog's optic tectum and pretectum. In J.-P. Ewert and M. A. Arbib (eds.), *Visuomotor Coordination: Amphibians, Comparisons, Models and Robots*. New York: Plenum, pp. 175–199.

Lázár, G. (2001) Peptides in frog brain areas processing visual information. *Microscop. Res. Techn.* 54: 201–219.

Lázár, G. and Kozicz, T. (1990) Morphology of neurons and axon terminals associated with descending and ascending pathways of the lateral forebrain bundle in *Rana esculenta*. *Cell Tiss. Res.* 260: 535–548.

Lázár, G., Tóth, P., Csank, G., and Kicliter, E. (1983b) Morphology and location of tectal projection neurons in frogs: A study with HRP and cobalt-filling. *J. Comp. Neurol.* 215: 108–120.

Lázár, G., Maderdrut, J. L., Trasti, S. L., Liposits, Z., Tóth, P., Kozicz, T., and Merchenthaler I. (1993) Distribution of proneuropeptide Y-derived peptides in the brain of *Rana esculenta* and *Xenopus laevis*. *J. Comp. Neurol.* 327: 551–571.

Lefebvre, L., Whittle, P., Lascaris, E., and Finkelstein, A. (1997) Feeding innovations and forebrain size in birds. *Anim. Behav.* 53: 549–560.

Leggett, L. M. W. (1976) Polarised light-sensitive neurons in a swimming crab. *Nature* (*London*) 262: 709–711.

Lehrer, M. (1998) Looking all around: Honeybees use different cues in different eye regions. *J. Exp. Biol.* 201: 3275–3292.

Lehrer, M., Horridge, G. A., Zhang, Z. W., and Gadagkar, R. (1995) Shape vision in bees: Innate preference for flower-like patterns. *Phil. Trans. Roy. Soc. Lond. B* 347: 123–137.

Leitinger, G. (1994) Frühe postembryonale Entwicklung des Komplexauges und der Lamina ganglionaris der Gottesanbeterin nach Photodegeneration der akuten Zone mit Sulforhodamin. Masters thesis, Univ. of Graz, Graz, Austria.

Leitinger, G. (1997) Serotonin-immunoreactive neurones in the visual system of larval and adult praying mantis (*Tenodera sinensis*). Ph.D. thesis, Univ. of Graz, Graz, Austria.

Leitinger, G., Pabst, M. A., and Kral, K. (1999) Serotonin-immunoreactive neurones in the visual system of the praying mantis: An immunohistochemical, confocal laser scanning and electron microscopic study. *Brain Res.* 823: 11–23.

Lettvin, J. Y., Maturana, H. R., McCulloch, W. S., and Pitts, W. H. (1959) What the frog's eye tells the frog's brain. *Proc. Inst. Radio. Engin.* 47: 1940–1951.

Leung, V. and Comer, C. M. (2001) Identification and characterization of a visual interneuron in the cockroach, *Periplaneta americana*, equivalent to DCMD. *Soc. Neurosci. Abstr.* vol. 27, Program No. 308.2.

Levine, J. S. (1980) Vision underwater. *Oceanus* 23: 19–26.

Li, D. and Jackson, R. R. (1996) Prey preferences of *Portia fimbriata*, an araneophagic, web-building jumping spider (Araneae: Salticidae) from Queensland. *J. Insect Behav.* 9: 613–642.

Li, D., Jackson, R. R., and Barrion, A. (1997) Prey preferences of *Portia labiata*, *P. africana* and *P. schultzi*, araneophagic jumping spiders (Araneae: Salticidae) from the Philippines, Sri Lanka, Kenya and Uganda. *NZ J. Zool.* 24: 333–349.

Li, D., Jackson, R. R., and Barrion, A. (1999) Parental and predatory behaviour of *Scytodes* sp., an araneophagic spitting spider (Araneae: Scytodidae) from the Philippines. *J. Zool. Lond.* 247: 293–310.

Li, Z., Fite, K. V., Montgomery, N. M., and Wang, S. R. (1996) Single-unit resoponses to whole-field visual stimulation in the pretectum of *Rana pipiens*. *Neurosci. Lett.* 218: 193–197.

Libersat, F. (1992) Modulation of flight by giant interneurons of the cockroach. *J. Comp. Physiol.* 170: 379–392.

Lima, P. A., Coehlo, M. L., Andrade, J. P., and Brown, E. R. (1995) Do squid school like fish? In A. Guerra, E. Rolán, and F. Rocha (eds.), *Abstracts of the 12th International Malacological Congress*, Vigo, Spain: Instituto de Investigaciones Marinas, pp. 70.

Lindauer, M. (1955) Schwarmbienen auf Wohnungssuche. *Z. Vergl. Physiol.* 37: 263–324.

Lindauer, M. (1959) Angeborene und erlernte Komponenten in der Son-nenorientierung der Bienen. *Z. Vergl. Physiol.* 42: 43–62.

Lindemann, B. (2001) Receptors and transduction in taste. *Nature* 413: 219–225.

Lindemann, S. O. G. and Roth, G. (1999) A fear acquisition system in amphibians. *Neural Plast.* 1: 65.

Lindsay, P. H. and Norman, D. A. (1977) *Human Information Processing: An Introduction to Psychology*. New York: Academic Press.

Liske, E. (1999) The hierarchical organization of mantid behavior. In F. R. Prete, H. Wells, P. Wells, and L. E. Hurd (eds.), *The Praying Mantids*. Baltimore, Md.: Johns Hopkins Univ. Press, pp. 224–250.

Little, E. E. (1975) Chemical communication in maternal behaviour of crayfish. *Nature* 255: 400–1.

Loi, P. K., Saunders, R. G., Young, D. C., and Tublitz, N. J. (1996) Peptidergic regulation of chromatophore function in the European cuttlefish *Sepia officinalis*. *J. Exp. Biol.* 199: 1177–1187.

Lubbock, J. (1889) Die Sinne und das Geistige Leben der Tiere. *Wissenschaftl. Bibliothek Band* 57.

Lucero, M. T. and Gilly, W. T. (1995) Physiology of squid olfaction. In N. J. Abbott, R. Williamson, and L. Maddock (eds.), *Cephalopod Neurobiology. Neuroscience Studies in Squid, Octopus and Cuttlefish*. Oxford: Oxford Univ. Press.

Lucero, M. T., Farrington, H., and Gilly, W. F. (1994) Quantification of L-dopa and dopamine in squid ink: Implications for chemoreception. *Biol. Bull.* 187: 55–63.

Lucero, M. T., Horrigan, F. T., and Gilly, W. F. (1992) Electrical responses to chemical stimulation of squid olfactory receptor cells. *J. Exp. Biol.* 162: 231–249.

Luksch, H. and Roth, G. (1996) Pretecto-tectal interactions: Effects of lesioning and stimulating the pretectum on field potentials in the optic tectum of salamanders in vitro. *Neurosci. Lett.* 217: 137–140.

Luksch, H., Kahl, H., Wiggers, W., and Roth, G. (1998) Connectivity of the salamander pretectum: An in-vitro (whole-brain) intracellular tracing study. *Cell Tiss. Res.* 292: 47–56.

Lunau, K. (1990) Colour saturation triggers innate reactions to flower signals: Flower dummy experiments with bumblebees. *J. Comp. Physiol. A* 166: 827–834.

Lunau, K., Wacht, S., and Chittka, L. (1996) Colour choices of naive bumble bees and their implications for colour perception. *J. Comp. Physiol. A* 178: 477–489.

Luthardt, G. and Roth, G. (1979) The role of stimulus movement patterns in the prey-catching behavior of *Salamandra salamandra*. *Copeia* 1979: 442–447.

Lythgoe, J. N. (1972) The adaptation of visual pigments to the photic environment. In H. J. A. Dartnall (ed.), *Handbook of Sensory Physiology*. VII/1, *Photochemistry of Vision*. Berlin: Springer-Verlag, pp. 566–603.

Lythgoe, J. N. (1976) Underwater vision. *Proc. Roy. Soc. Med.* 69: 67–68.

Lythgoe, J. N. (1979) *The Ecology of Vision*. Oxford: Clarendon Press.

Lythgoe, J. N. (1985) Aspects of photoreception in aquatic environments. *Symp. Soc. Exp. Biol.* 39: 373–386.

Lythgoe, J. N. and Hemming, C. C. (1967) Polarized light and underwater vision. *Nature* 213: 893–894.

Lythgoe, J. N. and Partridge, J. C. (1989) Visual pigments and the acquisition of visual information. *J. Exp. Biol.* 146: 1–20.

Mace, G. M., Harvey, P. H., and Clutton-Brock, T. M. (1981) Brain size and ecology in small mammals. *J. Zool. Lond.* 193: 333–354.

MacFarland, W. N. and Munz, F. W. (1975a) Part II: The photic environment of clear tropical seas during the day. *Vision Res.* 15: 1063–1070.

MacFarland, W. N. and Munz, F. W. (1975b) Part III: The evolution of photopic visual pigments in fishes. *Vision Res.* 15: 1071–1080.

Maddess, T., Dubois, R. A., and Ibbotson, M. R. (1991) Response properties and adaptation of neurones sensitive to image motion in the butterfly *Papilio aegeus*. *J. Exp. Biol.* 161: 171–199.

Magni, F., Papi, F., Savely, H. E., and Tongiorgi, P. (1964) Research on the structure and physiology of the eyes of a lycosid spider. II. The role of different pairs of eyes in astronomical orientation. *Archs. Ital. Biol.* 102: 123–136.

Magni, F., Papi, F., Savely, H. E., and Tongiorgi, P. (1965) Research on the structure and physiology of the eyes of a lycosid spider. III. Electroretinographic responses to polarised light. *Archs. Ital. Biol.* 103: 146–158.

Maldonado, H. (1970) The deimatic reaction in the praying mantis *Stagmatoptera biocellata*. *Z. Vergl. Physiol.* 68: 60–71.

Maloney, L. T. (1986) Evaluation of linear models of surface spectral reflectance with small numbers of parameters. *J. Opt. Soc. Am. A* 3: 1673–1683.

Maloney, L. T. and Wandell, B. A. (1986) Color constancy: A method for recovering surface spectral reflectance. *J. Opt. Soc. Am. A* 3: 29–33.

Manning, R. L. (1995) Stomatopod crustacea of Vietnam: The legacy of Raoul Serene. *Crustacean Research Special Number 4*. Carcinol. Soc. Japan, Tokyo.

Manning, R. L., Schiff, H., and Abbott, H. (1984) Eye structure and the classification of the stomatopod Crustacea. *Zool. Scripta*. 13: 41–44.

Marín, O., González, A., and Smeets, W. J. A. J. (1997a) Basal ganglia organization in amphibians: Efferent connections of the striatum and the nucleus accumbens. *J. Comp. Neurol.* 380: 23–50.

Marín, O., González, A., and Smeets, W. J. A. J. (1997b) Anatomical substrate of amphibian basal ganglia involvement in visuomotor behaviour. *Eur. J. Neurosci.* 9: 2100–2109.

Marín, O., Smeets, W. J. A. J., and González, A. (1997c) Basal ganglia organization in amphibians: Development of striatal and nucleus accumbens connections with emphasis on the catecholaminergic inputs. *J. Comp. Neurol.* 383: 349–369.

Marín, O., Smeets, W. J. A. J., and González, A. (1997d) Basal ganglia organization in amphibians: Catecholaminergic innervation of the striatum and the nucleus accumbens. *J. Comp. Neurol.* 378: 50–69.

Marín, O., González, A., and Smeets, W. J. A. J. (1998a) Basal ganglia organization in amphibians: Chemoarchitecture. *J. Comp. Neurol.* 392: 285–312.

Marín, O., Smeets, W. J. A. J., and González A. (1998b) Evolution of the basal ganglia in tetrapods: A new perspective based on recent studies in amphibians. *Trends Neurosci.* 21: 487–494.

Marín, O., Smeets, W. J. A. J., Munoz, M., Sanchez-Camacho, C., Pena, J. J., Lopez, J. M., and González, A. (1999) Cholinergic and catecholaminergic neurons relay striatal information to the optic tectum in amphibians. *Eur. J. Morphol.* 37: 155–159.

Marshall, N. J. (1988) A unique colour and polarisation vision system in mantis shrimps. *Nature* 333: 557–560.

Marshall, N. J. and Land, M. F. (1993a) Some optical features of the eyes of stomatopods. I. Eye shape, optical axis and resolution. *J. Comp. Physiol. A* 173: 565–582.

Marshall, N. J. and Land, M. F. (1993b) Some optical features of the eyes of stomatopods. II. Ommatidial design, sensitivity and habitat. *J. Comp. Physiol. A* 173: 583–594.

Marshall, N. J. and Messenger, J. B. (1996) Colour-blind camouflage. *Nature (London)* 382: 408–409.

Marshall, N. J. and Oberwinkler, J. (1999) The colourful world of the mantis shrimp. *Nature (London)* 401: 873–874.

Marshall, N. J., Land, M. F., King, C. A., and Cronin, T. W. (1991a) The compound eyes of mantis shrimps (Crustacea, Hoplocarida, Stomatopoda). I. Compound eye structure: The detection of polarized light. *Phil. Trans. Roy. Soc. Lond. B* 334: 33–56.

Marshall, N. J., Land, M. F., King, C. A., and Cronin, T. W. (1991b) The compound eye of mantis shrimps (Crustacea, Hoplocarida, Stomatopoda). II. Colour pigments in the eyes of stomatopod crustaceans: Polychromatic vision by serial and lateral filtering. *Phil. Trans. Roy. Soc. Lond. B* 334: 57–84.

Marshall, N. J., Land, M. F., and Cronin, T. W. (1994) The six-eyed stomatopod. *Endeavour* 18: 17–26.

Marshall, N. J., Jones, J. P., and Cronin, T. W. (1996) Behavioural evidence for color vision in stomatopod crustaceans. *J. Comp. Physiol. A* 179: 473–481.

Marshall, N. J., Cronin, T. W., and Shashar, N. (1999) Behavioural evidence for polarization vision in stomatopods reveals a potential channel for communication. *Curr. Biol.* 9: 755–758.

Masino, T. and Grobstein, P. (1989a) The organization of descending tectofugal pathways underlying orienting in the frog, *Rana pipiens*. I. Lateralization, parcellation and an intermediate spatial representation. *Exp. Brain Res.* 75: 227–244.

Masino, T. and Grobstein, P. (1989b) The organization of descending tectofugal pathways underlying orienting in the frog, *Rana pipiens*. II. Evidence for the involvement of a tecto-tegmento-spinal pathway. *Exp. Brain Res.* 75: 245–264.

Masino, T. and Grobstein, P. (1990) Tectal connectivity in the frog *Rana pipiens*: Tectotegmental projections and a general analysis of topographic organization. *J. Comp. Neurol.* 291: 103–127.

Mason, A. C. and Bailey, W. J. (1998) Ultrasound hearing and male-male competition in Australian katydids (Tettigoniidae, Zaprochilinae) with sexually dimorphic ears. *Physiol. Entomol.* 23: 139–149.

Mason, A. C., Morris G. K., and Hoy, R. R. (1999) Peripheral frequency mis-match in the primitive ensiferan *Cyphoderris monstrosa* (Orthoptera: Hagilidae). *J. Comp. Physiol. A* 184: 543–551.

Masters, W. M., Markl, H., and Moffat, A. J. M. (1986) Transmission of vibration in a spider's web. In W. A. Shear (ed.), *Spiders: Webs, Behavior and Evolution*. Stanford, Calif: Stanford Univ. Press, pp. 49–69.

Mathger, L. M. and Denton, E. J. (2001) Reflective properties of iridophores and fluorescent "eyespots" in the loliginid squid *Alloteuthis subulata* and *Loligo vulgaris*. *J. Exp. Biol.* 204: 2103–2118.

Matic, T. (1983) Electrical inhibition in the retina of the butterfly *Papilio*. I. Four spectral types of photoreceptors. *J. Comp. Physiol. A* 152: 169–182.

Matsui, S., Seidou, M., Uchiyama, I., Sekiya, N., Hiraki, K., Yoshihara, K., and Kito, Y. (1988) 4-hydroxyretinal, a new visual pigment chromophore found in the bioluminescent squid, *Watacenia scintillans*. *Biochem. Biophys. Acta.* 966: 370–374.

Matsumoto, N. (1989) Morphological and physiological studies of tectal and pretectal neurons in the frog. In J.-P. Ewert and M. A. Arbib (eds.), *Visuomotor Coordination: Amphibians, Comparisons, Models and Robots*. New York: Plenum, pp. 201–222.

Matsumoto, N., Schwippert, W. W., and Ewert, J.-P. (1986) Intracellular activity of morphologically identified neurons of the grass frog's optic tectum in response to moving configurational visual stimuli. *J. Comp. Physiol. A* 159: 721–739.

Matsumoto, N., Schwippert, W. W., Beneke, T. W., and Ewert, J.-P. (1991) Forebrain-mediated control of visually guided prey-catching in toads: Investigation of striato-pretectal connections with intracellular recording/labeling methods. *Behav. Proc.* 25: 27–40.

Matsushima, T., Satou, M., and Ueda, K. (1989) Medullary reticular neurons in the Japanese toad: Morphology and excitatory inputs from the optic tectum. *J. Comp. Physiol. A* 166: 7–22.

Mazokhin-Porshnyakov, G. A. (1966) Recognition of coloured objects by insects. In C. G. Bernhard (ed.), *The Functional Organization of the Compound Eye*. Oxford: Pergamon Press, pp. 163–170.

McFarland, D. and Bosser, T. (1993) *Intelligent Behavior in Animals and Robots*. Cambridge, Mass: MIT Press.

McIlwain, J. T. (1996) *An Introduction to the Biology of Vision*. Cambridge: Cambridge University Press.

Medina, L. and Reiner, A. (1995) Neurotransmitter organization and connectivity of the basal ganglia in vertebrates: Implications for the evolution of basal ganglia. *Brain, Behav. Evol.* 46: 235–258.

Medina, L., Jiao, Y., and Reiner, A. (1999) The functional anatomy of the basal ganglia in birds. *Eur. J. Morphol.* 37: 160–165.

Meier, T., Chabaud, F., and Reichert, H. (1991) Homologous patterns in the embryonic development of the peripheral nervous system in the grasshopper *Schistocera gregaria* and the fly *Drosophila melanogaster*. *Development* 112: 241–253.

Meinecke, C. C. and Langer, H. (1984) Localization of visual pigments within rhabdoms of the compound eye of *Spodoptera exempta* (Insecta, Noctuidae). *Cell Tiss. Res.* 238: 359–368.

Meinertzhagen, I. A. (1991) Evolution of the cellular organization of the arthropod compound eye and optic lobe. In J. R. Cronly-Dillon and R. L. Gregory (eds.), *Evolution of the Eye and Visual System: Vision and Visual Dysfunction*. New York: Macmillan, pp. 341–363.

Mengual, E., de las Heras, S., Erro, E., Lanciego, J. L., and Bimenez-Amaya, J. M. (1999) Thalamic interaction between the input and the output system of the basal ganglia. *J. Chem. Neuroanat.* 16: 187–200.

Menzel, R. (1979) Spectral sensitivity and colour vision in invertebrates. In H. Autrum (ed.), *Handbook of Sensory Physiology*. vol. VII/6A, *Invertebrate Photoreceptors*. Berlin: Springer-Verlag, pp. 503–580.

Menzel, R. (1985) Learning in honey bees in an ecological and behavioral context. In B. Hölldobler and M. Lindauer (eds.), *Experimental Behavioral Ecology*. Stuttgart: Gustav Fischer Verlag, pp. 55–74.

Menzel, R. (1990) Learning, memory and "cognition" in honey bees. In R. P. Kesner and D. S. Olton (eds.), *Neurobiology of Comparative Cognition*. Hillsdale, N.J.: IEA Publishers, pp. 237–292.

Menzel, R. (2001) Behavioral and neural mechanisms of learning and memory as determinants of flower constancy. In L. Chittka and J. D. Thomson (eds.), *Cognitive Ecology of Pollination*. Cambridge: Cambridge Univ. Press, pp. 21–40.

Menzel, R. and Backhaus, W. (1989) Color vision in honey bees: Phenomena and physiological mechanisms. In D. Stavenga and R. Hardie (eds.), *Facets of Vision*. Berlin: Springer-Verlag, pp. 281–297.

Menzel, R. and Backhaus, W. (1991) Colour vision in insects. In P. Gouras (ed.), *The Perception of Colour*. London: Macmillan, pp. 262–293.

Menzel, R. and Bitterman, M. E. (1983) Learning by honeybees in an unnatural situation. In F. Huber and H. Markl (eds.), *Neurobiology and Behavioral Physiology*. Berlin: Springer-Verlag, pp. 206–215.

Menzel, R. and Blakers, M. (1976) Colour receptors in the bee eye—Morphology and spectral sensitivity. *J. Comp. Physiol.* 108: 11–33.

Menzel, R. and Greggers, U. (1985) Natural phototaxis and its relationship to colour vision in honeybees. *J. Comp. Physiol.* 157: 311–321.

Menzel, R. and Lieke, E. (1983) Antagonistic color effects in spatial vision of honeybees. *J. Comp. Physiol. A* 151: 441–448.

Menzel, R. and Muller, U. (1996) Learning and memory in honeybees: From behavior to neural substrates. *Ann. Rev. Neurosci.* 19: 379–404.

Menzel, R., Bicker, G., Carew, T. J., Fischbach, K. F., Gould, J. L., Heinrich, B., Heisenberg, M. A., Lindauer, M., Markl, H. S., Quinn, W. G., Sahley, C. L., and Wagner, A. R. (1984) Biology of invertebrate learning. In P. Marler and H. S. Terrace (eds.), *The Biology of Learning: Report of the Dahlem Workshop on the Biology of Learning*. Berlin: Springer-Verlag, pp. 249–270.

Merchenthaler, I., Lázár, G., and Maderdrut, J. L. (1989) Distribution of proenkephalin-derived peptides in the brain of *Rana esculenta*. *J. Comp. Neurol.* 281: 23–39.

Meredith, M. A. and Stein, B. E. (1986) Visual, auditory and somato-sensory convergence on cells in superior colliculus results in multisensory integration. *J. Neurophysiol.* 75: 1843–1857.

Merkel-Harff, C. and Ewert, J.-P. (1991) Learning-related modulation of toad's responses to prey by neural loops involving the forebrain. In M. A. Arbib and J.-P. Ewert (eds.), *Visual Structures and Integrated Functions*. Berlin: Springer-Verlag, pp. 417–426.

Messenger, J. B. (1971) The optic tract lobes. In J. Z. Young (ed.), *The Anatomy of the Nervous System of Octopus vulgaris*. Oxford: Oxford Univ. Press, pp. 481–506.

Messenger, J. B. (1974) Reflective elements in cephalopod skin and their importance for camouflage. *J. Zool. Lond.* 174: 387–395.

Messenger, J. B. (1977) Evidence that Octopus is colour blind. *J. Exp. Biol.* 70: 49–55.

Messenger, J. B. (1979a) The nervous system of *Loligo* IV. The peduncle and olfactory lobes. *Phil. Trans. Roy. Soc. Lond. B* 285: 275–309.

Messenger, J. B. (1979b) The eyes and skin of Octopus: Compensating for sensory deficiencies. *Endeavour* 3: 92–98.

Messenger, J. B. (1981) Comparative physiology of vision in molluscs. In H. Autrum (ed.), *Handbook of Sensory Physiology*. vol. VII/6C, *Comparative Physiology and Evolution of Vision in Invertebrates*. Berlin: Springer-Verlag, pp. 93–200.

Messenger, J. B. (1991) Photoreception and vision in molluscs. In J. R. Cronly-Dillon and R. L. Gregory (eds.), *Evolution of the Eye and Visual System*. London: Macmillan, pp. 364–397.

Messenger, J. B. (2001) Cephalopod chromatophores: Neurobiology and natural history. *Biol. Rev. Camb. Phil. Soc.* 76: 473–528.

Messenger, J. B., Wilson, A. P., and Hedge, A. (1973) Some evidence for colour blindness in Octopus. *J. Exp. Biol.* 59: 77–94.

Meyer, D. J., Margiotta, J. F., and Walcott, B. (1981) The shadow response of the cockroach *Periplaneta americana*. *J. Neurobiol.* 12(1): 93–96.

Meyer-Rochow, V. B. and Eguchi, E. (1984) The effects of temperature and light on particles associated with crayfish visual membrane: A freeze-fracture analysis and electrophysiological study. *J. Neurocytol.* 13: 935–959.

Michinomae, M., Masuda, H., Seidou, M., and Kito, Y. (1994) Structural basis for wavelength discrimination in the banked retina of the firefly squid, *Watasenia scintillans*. *J. Exp. Biol.* 193: 1–12.

Miller, J. P., Jacobs, G. A., and Theunissen, F. E. (1991) Representation of sensory information in the cricket cercal sensory system I. Response properties of the primary interneurons. *J. Neurophysiol.* 66: 1680–1689.

Miller, W. H. (1979) Ocular optical filtering. In H. Autrum (ed.), *Handbook of Sensory Physiology*. Vol. VII/6C, *Comparative Physiology and Evolution of Vision in Invertebrates*. Berlin: Springer-Verlag, pp. 69–143.

Mitaku, T. (1951) The distribution of two species of crayfish imported from America in Japan (in Japanese). *Zool. Sci.* 68: 124.

Mittelstaedt, H. (1962) Control systems of orientation in insects. *Ann. Rev. Ent.* 7: 177–198.

Mize, R. (1983) Patterns of convergence and divergence of retinal and cortical synaptic terminals in the cat superior colliculus. *Exp. Brain Res.* 269: 211–221.

Mizrahi, A. and Libersat, F. (1997) Independent coding of wind direction in cockroach giant interneurons. *J. Neurophysiol.* 78(5): 2655–2661.

Mizunami, M. (1995) Morphology of higher-order ocellar interneurons in the cockroach brain. *J. Comp. Neurol.* 362: 293–304.

Montgomery, N. M. and Fite, K. V. (1991) Organization of ascending projections from the optic tectum and mesencephalic pretectal gray in *Rana pipiens*. *Vision Neurosci.* 7: 459–478.

Montgomery, N. M., Fite, K. V., Taylor, M., and Bengston, L. (1982) Neural correlates of optokinetic nystagmus in the mesencephalon of *Rana pipiens*: Functional analysis. *Brain, Behav. Evol.* 21: 137–150.

Montgomery, N. M., Fite, K. V., and Li, Z. (1991) Anatomical evidence for an intergeniculate leaflet in *Rana pipiens*. *Neurosci. Lett.* 133: 105–108.

Moody, M. F. (1962) Evidence for the intraocular discrimination of vertically and horizontally polarized light by Octopus. *J. Exp. Biol.* 39: 21–30.

Moody, M. F. and Parriss, J. R. (1960) Discrimination of polarized light by Octopus. *Nature* 186: 839–840.

Moody, M. F. and Parriss, J. R. (1961) The discrimination of polarized light by Octopus: A behavioral and morphological study. *Z. Vergl. Physiol.* 44: 268–291.

Moran, M. D. and Hurd, L. E. (1994) Environmentally determined male-biased sex ratio in a praying mantid. *Am. Midl. Nat.* 132: 205–208.

Morton, E. S. (1975) Ecological sources of selection on avian sounds. *Am. Nat.* 109: 17–34.

Muntz, W. R. A. (1962a) Microelectrode recordings from the diencephalon of the frog (*Rana pipiens*) and a blue-sensitive system. *J. Neurophysiol.* 25: 699–711.

Muntz, W. R. A. (1962b) Effectiveness of different colours of light in releasing the positive phototactic behavior of frogs and a possible function of the retinal projection to the diencephalon. *J. Neurophysiol.* 25: 712–720.

Muntz, W. R. A. (1977a) Pupillary response of cephalopods. *Symp. Zool. Soc. Lond.* 38: 277–285.

Muntz, W. R. A. (1977b) The visual world of amphibia. In H. Autrum, R. Jung, W. R. Loewenstein, D. M. McKay, and H. L. Teuber (eds.), *Handbook of Sensory Physiology*. vol. VII/5, *The Visual System in Vertebrates*. Berlin: Springer-Verlag, pp. 275–307.

Muntz, W. R. A. and Gwyther, J. (1988) Visual acuity in *Octopus pallidus* and *Octopus australis*. *J. Exp. Biol.* 134: 119–129.

Muntz, W. R. A. and Johnson, M. S. (1978) Rhodopsins of oceanic decapods. *Vision Res.* 18: 601–602.

Nagel, T. (1974) What is it like to be a bat? *Phil. Rev.* 83(4): 435–450.

Naguib, M. and Wiley, R. H. (2001) Estimating the distance to a source of sound: Mechanisms and adaptations for long-range communication. *Anim. Behav.* 62: 825–837.

Nakamura, T. and Yamashita, S. (2000) Learning and discrimination of colored papers in jumping spiders (Araneae, Salticidae). *J. Comp. Physiol. A* 186: 897–901.

Narins, P. M. (1995) Frog communication. *Sci. Am.* 273: 78–83.

Nasi, E., Pilar Gomez, M., and Payne, R. (2000) Phototransduction mechanisms in microvillar and ciliary photoreceptors of invertebrates. In D. G. Stavenga, W. J. DeGrip, and E. N. Pugh (eds.), *Handbook of Biological Physics*. vol. 3, *Molecular Mechanisms in Visual Transduction*. Amsterdam: Elsevier, pp. 389–448.

Neary, T. J. (1990) The pallium of anuran amphibians. In E. G. Jones and A. Peters (eds.), *Comparative Structure and Evolution of Cerebral Cortex, Part I: Cerebral Cortex*, vol. 8A, New York: Plenum, pp. 107–138.

Neary, T. J. and Northcutt, R. G. (1983) Nuclear organization of the bullfrog diencephalon. *J. Comp. Neurol.* 213: 262–278.

Nel, A. and Roy, R. (1996) Revision of the fossil "mantid" and "ephemerid" species described by Piton from the Paleocene of Menat (France) (Mantodea: Chaeteessidae, Mantidae; Ensifera: Tettigonioidea) *Eur. J. Entomol.* 93: 223–234.

Nelson, B. S. and Stoddard, P. K. (1998) Accuracy of auditory distance and azimuth perception by a passerine bird in natural habitat. *Anim. Behav.* 56: 467–477.

Nesis, K. N. (1974) Cuttlefishes catch prey in the air. *Priroda* 1974(5): 107–109 (in Russian).

Neumeyer, C. (1981) Chromatic adaptation in honeybee: Successive color contrast and color constancy. *J. Comp. Physiol. A* 144: 543–553.

Neumeyer, C. (1991) Evolution of colour vision. In J. R. Cronly-Dillon and R. L. Gregory (eds.), *Vision and Visual Dysfunction: Evolution of the Eye and Visual System*, vol. 2. London: Macmillan, pp. 284–305.

Neumeyer, C. (1998) Color vision in lower vertebrates. In W. G. K. Backhaus, R. Kliegl, and J. S. Werner (eds.), *Color Vision: Perspectives from Different Disciplines*. Berlin, New York: Walter de Gruyter, pp. 149–162.

Neumeyer, C. and Kitschmann, M. (1998) Color categories in goldfish and humans. *Invest. Ophthal. Vision Sci.* 39: 155.

Neville, A. C. and Luke, B. M. (1971) Form optical activity in crustacean cuticle. *J. Insect Physiol.* 17: 519–526.

Nicklaus, R. (1965) Die Erregung einzellner Fadenhaare von *Periplaneta americana* in abhängigkeit von der Grösse und Richtung der Auslenkung. *Z. Vergl. Physiol.* 50: 331–362.

Nickle, D. A. (1981) Predation on a mouse by the Chinese mantid *Tenodera aridifolia sinensis*, Saussure (Dictyoptera: Mantoidea). *Proc. Ent. Soc. Wash.* 83: 802–803.

Nilsson, D.-E. (1983) Evolutionary links between apposition and superposition optics in crustacean eyes. *Nature (London)* 302: 818–821.

Nilsson, D.-E. (1989) Optics and evolution of the compound eye. In D. G. Stavenga and R. C. Hardie (eds.), *Facets of Vision*. Berlin: Springer-Verlag, pp. 30–73.

Nilsson, D.-E. and Warrant, E. J. (1999) Visual discrimination: Seeing the third quality of light. *Curr. Biol.* 9: R535–R357.

Nilsson, D.-E., Labhart, T., and Meyer, E. (1987) Photoreceptor design and optical properties affecting polarization sensitivity in ants and crickets. *J. Comp. Physiol. A* 161: 645–658.

Nilsson, D.-E., Land, M. F., and Howard, J. (1988) Optics of the butterfly eye. *J. Comp. Physiol. A* 162: 341–366.

Nishikawa, K. C. (1999) Neuromuscular control of prey capture in frogs. *Phil. Trans. Roy. Soc. Lond. B. Sci.* 354: 941–954.

Nishikawa, K. C. and Gans, C. (1992) The role of hypoglossal sensory feedback during feeding in the marine toad, *Bufo marinus*. *J. Exp. Zool.* 264: 245–252.

Nishikawa, K. C., Roth, G., and Dicke, U. (1991) Motor neurons and motor columns of the anterior spinal cord of salamanders: Posthatching development and phylogenetic distribution. *Brain, Behav. Evol.* 37: 368–382.

Nishikawa, K. C., Anderson, C. W., Deban, S. M., and O'Reilly, J. C. (1992) The evolution of neural circuits controlling feeding behavior in frogs. *Brain, Behav. Evol.* 40: 125–140.

Norman, M. D. (2000) *Cephalopods, a World Guide*. Hackenheim, Germany: ConchBooks.

Norman, M. D., Finn, J., and Tregenza, T. (2001) Dynamic mimicry in an Indo-Malayan octopus. *Proc. Roy. Soc. Lond. B* 268: 1755–1758.

Northcutt, R. G. and Ronan, M. (1992) Afferent and efferent connections of the bullfrog medial pallium. *Brain, Behav. Evol.* 40: 1–16.

Norton, A. C., Fukada, Y., Motokawa, K., and Tasaki, K. (1965) An investigation of the lateral spread of potentials in the octopus retina. *Vision Res.* 5: 253–267.

Nosaki, H. (1969) Electrophysiological study of color encoding in the compound eye of crayfish, *Procambarus clarkia*. *Z. vergl. Physiol.* 64: 318–323.

Obara, Y. and Majerus, M. E. N. (2000) Initial mate recognition in the British cabbage butterfly, *Pierisrapae rapae*. *Zool. Sci.* 17: 725–730.

Okada, J. and Toh, Y. (2000) The role of antennal hair plates in object-guided tactile orientation of the cockroach (*Periplaneta americana*). *J. Comp. Physiol. A* 186: 849–857.

Okada, J. and Toh, Y. (2001) Peripheral representation of antennal orientation by the scapal hair plate of the cockroach *Periplaneta americana*. *J. Exp. Biol.* 204: 4301–4309.

Okano, T., Fukada, Y., and Yoshizawa, T. (1995) Molecular basis for tetrachromatic color vision. *Comp. Biochem. Physiol. B* 112: 405–414.

Olivo, R. F. and Larsen, M. E. (1978) Brief exposure to light intensities screening pigment migration in retinula cells of the crayfish, *Procambarus*. *J. Comp. Physiol.* 125: 91–96.

O'Shea, M. and Rowell, C. H. F. (1976) The neuronal basis of a sensory analyzer, the acridid movement detector system. II. Response decrement, convergence and the nature of the excitatory afferents to the fan-like dendrites of the LGMD. *J. Exp. Biol.* 65: 289–308.

O'Shea, M., Rowell, C. H. F., and Williams, J. L. D. (1974) The anatomy of a locust visual interneurone: The descending contralateral movement detector. *J. Exp. Biol.* 60: 1–12.

Osorio, D. (1986) Directionally selective cells in the locust medulla. *J. Comp. Physiol. A* 159: 841–847.

Osorio, D., Averof, M., and Bacon, J. P. (1995) Arthropod evolution: Great brains, beautiful bodies. *Ecol. Evol.* 10: 449–454.

Osorio, D., Marshall, N. J., and Cronin, T. W. (1997) Stomatopod photoreceptor spectral tuning as an adaptation for colour constancy in water. *Vision Res.* 37: 3299–3309.

Otis, T. and Gilly, W. F. (1990) Jet-propelled escape in the squid *Loligo opalescens*: Concerted control by giant and non-giant motor axon pathways. *Proc. Nat. Acad. Sci. U.S.A* 87: 2911–2915.

O'Tousa, J. E., Baehr, W., Martin, R. L., Hirsch, J., Pak, W. L., and Applebury, M. L. (1985) The *Drosophila* ninaE gene encodes an opsin. *Cell* 40: 839–850.

Ott, M., Schaeffel, F., and Kirmse, W. (1998) Binocular vision and accommodation in prey-catching chameleons. *J. Comp. Physiol. A* 182: 319–330.

Packard, A. (1969a) Operational convergence between cephalopods and fish: An exercise in functional anatomy. *Arch. Zool. Ital.* 51: 523–542.

Packard, A. (1969b) Visual acuity and eye growth in *Octopus vulgaris* (Lamarck). *Monitore. Zool. Ital.* 3: 19–32.

Packard, A. (1972) Cephalopods and fish: The limits of convergence. *Biol. Rev.* 47: 241–307.

Packard, A. (1995) Organization of cephalopod chromatophore systems: A neuromuscular image-generator. In N. J. Abbott, R. Williamson, and L. Maddock (eds.), *Cephalopod Neurobiology. Neuroscience Studies in Squid, Octopus and Cuttlefish*. Oxford: Oxford Univ. Press, pp. 331–367.

Packard, A. and Hochberg, F. G. (1977) Skin patterning in Octopus and other genera. *Sym. Zool. Soc. Lond.* 38: 191–231.

Packard, A. and Sanders, G. D. (1969) What the octopus shows to the world. *Endeavour* 28: 992–999.

Palka, J. (1967) An inhibitory process influencing visual responses in a fiber of the ventral nerve cord of locusts. *J. Insect Physiol.* 41: 235–248.

Papini, M. R., Muzio, R. N., and Segura, E. T. (1995) Instrumental learning in toads (*Bufo arenarum*): Reinforcer magnitude and the medial pallium. *Brain, Behav. Evol.* 46: 61–71.

Partridge, J. C. (1989) The visual ecology of avian cone oil droplets. *J. Comp. Physiol. A* 165: 415–426.

Patton, P. and Grobstein, P. (1998a) The effects of telencephalic lesions on the visually mediated prey orienting behavior in the leopard frog (*Rana pipiens*). I. The effects of complete removal of one telencephalic lobe, with a comparison to the effect of unilateral tectal lobe lesions. *Brain, Behav. Evol.* 51: 123–143.

Patton, P. and Grobstein, P. (1998b) The effects of telencephalic lesions on the visually mediated prey-orienting behavior in the leopard frog (*Rana pipiens*). II. The effects of limited lesions to the telencephalon. *Brain, Behav. Evol.* 51: 144–161.

Pearson, K. G. and O'Shea, M. (1984) Escape behavior of the locust. The jump and its initiation by visual stimuli. In R. C. Eaton (ed.), *Neural Mechanisms of Startle Behavior*. New York: Plenum, pp. 163–178.

Peaslee, A. G. and Wilson, G. (1989) Spectral sensitivity in jumping spiders (Araneae, Salticidae). *J. Comp. Physiol. A* 164: 359–363.

Peckham, G. W. and Peckham, E. G. (1887) Some observations on the mental powers of spiders. *J. Morphol.* 1: 383–419.

Peitsch, D., Fietz, A., Hertel, H., de Souza, J., Ventura, D. F., and Menzel, R. (1992) The spectral input systems of hymenopteran insects and their receptor-based colour vision. *J. Comp. Physiol. A* 170: 23–40.

Perez, S. M., Taylor, O. R., and Jander, R. (1997) A sun compass in monarch butterflies. *Nature* 387: 29.

Pettigrew, J. D. and Collin, S. P. (1995) Terrestrial optics in an aquatic eye: The sandlance, *Limnichthytes fasciatus* Creediidae, Teleostei. *J. Comp. Physiol. A* 177: 397–408.

Pflüger, H. J. and Field, L. H. (1999) A locust chordotonal organ coding for proprioceptive and acoustic stimuli. *J. Comp. Physiol.* 184: 169–183.

Pick, C. G. and Yanai, J. (1983) Eight arm maze for mice. *Int. J. Neurosci.* 21: 63–66.

Piercy, J. E., Embleton, T. F. W., and Sutherland, L. C. (1977) Review of noise propagation in the atmosphere. *J. Acoust. Soc. Am.* 61: 1402–1418.

Plummer, M. R. and Camhi, J. M. (1981) Discrimination of sensory signals from noise in the escape system of the cockroach: The role of wind acceleration. *J. Comp. Physiol.* 142: 347–357.

Pollack, G. S. and Imaizumi, K. (1999) Neural analysis of sound frequency in insects. *BioEssays* 21: 295–303.

Pollard, S. D., Macnab, A. M., and Jackson, R. R. (1987) Communication with chemicals: Pheromones and spiders. In W. Nentwig (ed.), *Ecophysiology of Spiders*. Heidelberg: Springer-Verlag, pp. 133–141.

Porter, K. R. (1972) *Herpetology*. Philadelphia, Pa.: Saunders.

Poteser, M. and Kral, K. (1995) Visual distance discrimination in praying mantis larvae: An index of the use of motion parallax. *J. Exp. Biol.* 198: 2127–2137.

Poteser, M., Pabst, M. A., and Kral, K. (1998) Proprioceptive contribution to distance estimation by motion parallax in a praying mantid. *J. Exp. Biol.* 201: 1483–1491.

Prazdny, K. (1985) Detection of binocular disparities. *Biol. Cybern.* 52: 93–99.

Prete, F. R. (1992a) Discrimination of visual stimuli representing prey versus non-prey by the praying mantis *Sphodromantis lineola* (Burr.). *Brain, Behav. Evol.* 39: 285–288.

Prete, F. R. (1992b) The effects of background pattern and contrast on prey discrimination by the praying mantis *Sphodromantis lineola* (Burr.). *Brain, Behav. Evol.* 40: 311–320.

Prete, F. R. (1993) Stimulus direction and retinal image location affect appetitive responses to computer-generated stimuli by the praying mantis *Sphodromantis lineola* (Burr.). *Vis. Neurosci.* 10: 997–1005.

Prete, F. R. (1999) Prey Recognition. In F. R. Prete, H. Wells, P. Wells, and L. E. Hurd (eds.), *The Praying Mantids*. Baltimore, Md.: Johns Hopkins Univ. Press, pp. 141–179.

Prete, F. R. and Cleal, K. (1996) The predatory strike of free ranging praying mantises, *Sphodromantis lineola* (Burr.) I: Strikes in the midsagittal plane. *Brain, Behav. Evol.* 48: 173–190.

Prete, F. R. and Mahaffey, R. J. (1993) Appetitive responses to computer-generated visual stimuli by the praying mantis *Sphodromantis lineola* (Burm.). *Vis. Neurosci.* 10: 669–679.

Prete, F. R. and Mclean, T. (1996) Responses to moving small-field stimuli by the praying mantis, *Sphodromantis lineola* (Burmeister). *Brain, Behav. Evol.* 47: 42–54.

Prete, F. R. and Wolf, M. M. (1992) Religious supplicant, seductive cannibal, or reflex machine? In search of the praying mantis. *J. Hist. Biol.* 25: 91–136.

Prete, F. R., Klimek, C. A., and Grossman, S. P. (1990) The predatory strike of the praying mantis, *Tenodera aridifolia sinensis* (Sauss.). *J. Insect. Physiol.* 36: 561–565.

Prete, F. R., Lum, H., and Grossman, S. P. (1992) Non-predatory ingestive behaviors of the praying mantids *Tenodera aridifolia sinensis* (Sauss.) and *Sphodromantis lineola* (Burm.). *Brain, Behav. Evol.* 39: 124–132.

Prete, F. R., Placek, P. J., Wilson, M. A., Mahaffey, J., and Nemcek, R. R. (1993) Stimulus speed and order of presentation effect the visually released predatory behaviors of the praying mantis *Sphodromantis lineola* (Burm.). *Brain, Behav. Evol.* 42: 281–294.

Prete, F. R., Hurd, L. E., Branstrator, D., and Johnson, A. (2002) Responses to computer-generated visual stimuli by the male praying mantis, *Sphodromantis lineola* (Burmeister). *Anim. Behav.* 63: 503–510.

Prete, F. R., Wells, H., Wells, P., and Hurd, L. E. (eds.) (1999) *The Praying Mantids*. Baltimore: Johns Hopkins University Press.

Preuss, T. and Budelmann, B. U. (1995a) A dorsal light reflex in a squid. *J. Exp. Biol.* 198: 1157–1159.

Preuss, T. and Budelmann, B. U. (1995b) Proprioceptive hair cells on the neck of the squid *Lolliguncula brevis*: A sense organ in cephalopods for the control of head-to-body position. *Phil. Trans. Roy. Soc. Lond. B* 349: 153–178.

Prier, K. R. (1999) The axonal projections and central connections of a set of serially repeating sensory organs in the locust, *Schistocerca gregaria*. Doctoral dissertation, University of Basel, Switzerland.

Prier, K. R. and Boyan, G. S. (2000) Synaptic input from serial chordotonal organs onto segmentally homologous interneurons in the grasshopper *Schistocerca gregaria*. *J. Insect Physiol.* 46: 298–312.

Pumphrey, R. J. (1961) Concerning vision. In J. A. Ramsay and V. B. Wigglesworth (eds.), *The Cell and the Organism. Essays Presented to Sir James Gray*. Cambridge: Cambridge Univ. Press, pp. 193–208.

Qiu, X. and Arikawa, K. (2003) The photoreceptor localization confirms the spectral heterogeneity of ommatidia in the male small white butterfly, *Pieris rapae crucivora*. *J. Comp. Physiol. A* 189: 81–88.

Qiu, X., Vanhoutte, K. A. J., Stavenga, D. G., and Arikawa, K. (2002) Ommatidial heterogeneity in the compound eye of the male small white butterfly, *Pieris rapae crucivora*. *Cell Tiss. Res.* 307: 371–379.

Raguso, R. A. (2001) Floral scent, olfaction and scent-driven foraging behavior. In L. Chittka and J. D. Thomson (eds.), *Cognitive Ecology of Pollination*. Cambridge: Cambridge Univ. Press, pp. 83–105.

Rashotte, M. E. (1987) Behavior in relation to objects in space: Some historical perspectives. In P. Ellen and C. Thinus-Blanc (eds.), *Cognitive Processes and Spatial Orientation in Animals and Man*. Dordrecht, Netherlands: Martinus Nijhoff, pp. 97–106.

Ratliff, F. (1976) On the psychophysiological bases of universal color terms. *Proc. Am. Phil. Soc.* 120: 311–330.

Regan, B. C., Julliot, C., Simmen, B. Viénot, F., Charles-Dominique, P., and Mollon, J. D. (2001) Fruits, foliage and the evolution of primate colour vision. *Phil. Trans. Roy. Soc. Lond. B* 356: 229–283.

Regolin, L., Vallortigara, G., and Zanforlin, M. (1994) Perceptual and motivational aspects of detour behaviour in young chicks. *Anim. Behav.* 47: 123–131.

Regolin, L., Vallortigara, G., and Zanforlin, M. (1995a) Object and spatial representations in detour problems by chicks. *Anim. Behav.* 49: 195–199.

Regolin, L., Vallortigara, G., and Zanforlin, M. (1995b) Detour behaviour in the domestic chick: Searching for a disappearing prey or a disappearing social partner. *Anim. Behav.* 50: 203–211.

Rehbein, H. G. (1976) Auditory neurons in the ventral cord of the locust; orphological and functional properties. *J. Comp. Physiol. A* 110: 233–250.

Reiner, A. (1987) The distribution of proenkephalin-derived peptides in the central nervous system of turtles. *J. Comp. Neurol.* 259: 65–91.

Reiner, A., Brauth, S. E., and Karten, H. J. (1980) Basal ganglionic pathways to the tectum: Studies in reptiles. *J. Comp. Neurol.* 193: 565–589.

Reiner, A., Karten, H. J., and Brecha, N. C. (1982a) Enkephalin-mediated basal ganglia influences over the optic tectum: Immunohistochemistry of the tectum and the lateral spiriform nucleus in pigeon. *J. Comp. Neurol.* 208: 37–53.

Reiner, A., Brecha, N. C., and Karten, H. J. (1982b) Basal ganglia pathways to the tectum: The afferent and efferent connections of the lateral spiriform nucleus of pigeon. *J. Comp. Neurol.* 208: 16–36.

Reiner, A., Brauth, S. E., and Karten, H. J. (1984) Evolution of the amniote basal ganglia. *Trends Neurosci.* 7: 320–325.

Reiner, A., Medina, L., and Veenman, C. L. (1998) Structural and functional evolution of the basal ganglia in vertebrates. *Brain Res. Rev.* 28: 235–285.

Rensch, B. (1956) Increase in learning capability with increase of brain-size. *Am. Nat.* 90: 81–95.

Reuther, T. and Virtanen, K. (1972) Border and colour coding in the retina of the frog. *Nature* 239: 260–263.

Ribi, W. A. (1978a) Colour receptors in the eye of the digger wasp, *Sphex cognatus* Smith: Evaluation by selective adaptation. *Cell Tiss. Res.* 195: 471–483.

Ribi, W. A. (1978b) A unique hymenopteran compound eye. The retina fine structure of the digger wasp *Sphex cognatus* Smith (Hymenoptera, Sphecidae). *Zool. Jb. Anat. Bd.* 100: 299–342.

Richman, D. B. and Jackson, R. R. (1992) A review of the ethology of jumping spiders (Araneae, Salticidae). *Bull. Br. Arachnol. Soc.* 9: 33–37.

Ridpath, M. G. (1977) Predation on frogs and small birds by *Hierodula werneri* (G.T) (Mantidae) in tropical Australia. *J. Aust. Ent. Soc.* 16: 153–154.