Chapter 10
Distributed Vision in Spiders

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Abstract We examine the distributed visual system of spiders, an ancient and diverse lineage of predators. Across families, prey-capture strategies include active pursuit, sit-and-wait predation, and the use of prey-capture webs. Spiders also have rich communicatory repertoires, using visual, vibratory, and chemical signals to communicate with potential mates, rivals, and social partners. Some species even demonstrate impressive problem-solving capabilities. Accompanying this behavioral diversity is impressive morphological variation, especially with respect to their visual systems. This variation includes the size of the eyes and their arrangement, eye anatomy and optical properties, photoreceptor structure, and underlying brain neuromorphology. Spiders have up to four pairs of "camera-type" eyes, any of which can exhibit specializations to overcome specific visual challenges. In this chapter, we will first examine vision in a well-studied family: the elegant, compact, and tightly integrated distributed visual system of jumping spiders (family Salticidae). From this example, we then expand our scope to a review of other spider families' vision while making the case for the importance of additional phylogenetically informed work.

Keywords Spider vision · Jumping spiders · Salticids · Principal eyes · Eye movements · Retinal specializations · Visual acuity · Visual sensitivity

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10.1 Why Spiders?

Spiders provide a stellar opportunity for studying the evolution of a distributed visual system. Most members of this group, the Araneae, have eight eyes, but beyond that, there is extraordinary diversity in everything from their visual ecology and eye arrangement to their eye function and the underlying neural circuitry. To illustrate this diversity, first consider the jumping spiders (family Salticidae). Charismatic, alert, and reactive, quickly pivoting to direct their prominent anterior-facing eyes at an approaching human, jumping spiders have been a natural object of study for behavioral scientists for many years. Take, for example, this description of the courtship display of a jumping spider by two pioneers in the study of salticid behavior, George and Elizabeth Peckham, in the late 1800s:

> On the first day of June of the present year we were so fortunate as to discover on a hot, stony hillside, large numbers of males and females of a new species of *Habrocestum* having a modification of the third leg… As it was their mating season, we had now a welcome opportunity of seeing what use the active little male, which is further beautified by having his first legs of a delicate light green color, with a fringe of white hairs along the outer side, makes of this adornment in paying his addresses to the female. When they are put into a mating-box together, the male notices the female at a distance of from six to eight inches, and rapidly approaches her. When within three or four inches, he begins to move from side to side, with his handsome first legs pointed downward and somewhat outward, his palpi [small appendages near the mouth used in sperm transfer] extended parallel with them, and his third legs raised above the first and second in such a way as to show the apophyses on the patellae. Frequently, in these preliminary movements, he bends the ends of the first legs inward—the bend being at the tibia—so as to put them into the form of a diamond, meanwhile moving the palpi rapidly up and down. As he approaches the female, she all the time eying him most intently, he raises the first pair of legs, swaying them backward and forward, still keeping the third pair well up, seeming as eager to display them as the first pair. In this way he approaches to within about two inches, when she rushes at him and he retreats. The whole performance is repeated (Peckham and Peckham 1890).

How can one fail to be charmed? It is no wonder that jumping spider vision has attracted a growing number of researchers, especially as novel techniques emerge. But what is also remarkable is how different other spider families can be. For many years, one of us (EMJ) had studied pholcids—typical cobweb spiders that one might find in the basement. Pholcids seem driven by vibration, easily fooled into thinking they have captured a fly by a tuning fork touching their web, but they barely react to changes in light. Other families illustrate yet more permutations: wolf spiders court with vibratory and visual signals, crab spiders wait on flowers to grab their prey, and net-casting and bolas spiders snatch their prey from the air. Thus, across spiders, we find an extraordinary diversity of visual capabilities and visually driven behaviors; the potential for comparative studies is enormous and has barely been tapped.

In this chapter, we will begin with a deep dive into salticids because of a particularly rich literature on jumping spider behavior and visual ecology, not to mention our own research interests. Next, we expand our view across the Araneae, in which we contextualize key concepts about spider vision. Throughout, we have tried to include enough detailed explanations to satisfy arachnologists who are new to vision research as well as visual ecologists who are new to spiders.

10.2 Jumping Spiders: A High-Performing, Compact Distributed Visual System

We begin by focusing on the Salticidae, whose visual systems have been studied far more than those of other spider families and thus can serve as a point of comparison later in the chapter. With the advent of exciting new techniques, recent years have seen a spike in the number of laboratories around the world devoted to studying jumping spider vision. Excellent and detailed primers on jumping spider vision are available (Harland and Jackson 2004; Harland et al. 2012; Land and Nilsson 2012; Morehouse et al. 2017; Morehouse 2020; Hill 2022). We especially wish to acknowledge the contributions of Michael Land, who became interested in salticids as a graduate student at Berkeley in the 1960s. His work forms the foundation for much of what we know about jumping spider vision (reviewed in Jackson and Harland 2009) and directly inspired much of our own work (e.g., Jakob et al. 2018; Zurek et al. 2015). In this section, we briefly describe first the interesting range of visually based behavior demonstrated by salticids, and then how that behavior is enabled by their distributed visual system. We begin our discussion with a historical context outlining how the field has approached the study of jumping spider vision and conclude with an overview of physiological techniques, only recently applied to spiders, that can be incorporated into tests of hypotheses about visual function.

10.2.1 Vision-Based Behavior of Jumping Spiders

10.2.1.1 Methods for Studying Vision-Based Behavior in Jumping Spiders

In order to understand spider vision, it is essential to first grasp its function. To this end, behaviorists have developed increasingly elegant methods for interrogating visually guided behaviors and associated cues. For example, to identify which visual features spiders attend to when classifying an object as conspecific, prey, or predator, researchers create flat or three-dimensional stimuli and observe the spiders' responses (e.g., Crane 1949; Drees 1952; Forster 1985; Harland and Jackson 2000; Rößler et al. 2021). Jumping spiders will display to their own reflection, and thus one can quantify the distance at which they can visually identify their reflection as a spider (Harland et al. 1999). To determine how spiders orient toward and track moving stimuli, spiders, like many insects (e.g., Taylor et al. 2015), can be tethered so that they would walk on a trackball that reconstructs their fictive path. Spiders attempting to turn toward a visual stimulus will rotate the trackball (e.g., Zurek et al. 2010; De Agrò et al. 2021), thereby allowing researchers to probe visual functions, like motion perception, spatial acuity, and contrast thresholds. A particularly valuable discovery came about by accident. One night, while watching a video of courtship behavior in the lab, David Clark noticed that a female spider was also watching the display. When Clark scaled down the video to life size, the female approached it and gave a receptive signal (D. Clark, personal communication). Clark and Uetz (1990) went on to show that spiders did not appear to distinguish between living crickets and a live video feed of those crickets. Since then, there has been widespread use of video playback and animation techniques in jumping spider studies, including in our own labs, to study courtship, predation, and other behaviors (a few examples of many include Clark and Morjan 2001; Harland and Jackson 2002; Bednarski et al. 2012; McGinley and Taylor 2016). Particularly ingenious is a virtual reality setup in which tethered spiders on a trackball navigate through a digital environment; in a virtual world they approach beacons indicating the location of their nest sites (Peckmezian and Taylor 2015a) just as they do in the field (Hoefler and Jakob 2006). Finally, the development of a spider-specific eye tracker (Canavesi et al. 2011, based on a design by Land 1969b) allows the precise measurement of the gaze direction of spiders as they view video stimuli, possible even while simultaneously recording their brain activity (Menda et al. 2014).

10.2.1.2 Behavioral Contexts in Which Jumping Spiders Use Vision

Jumping spider predatory behavior is highly visual and especially amenable to study, allowing researchers to probe the visual cues that these animals use to detect, identify, and respond to potential prey. Jumping spiders do not build prey-capture webs but are cat-like hunters, stalking and pouncing upon insects and smaller spiders (reviewed in Forster 1982; Jackson and Pollard 1996). They attack even unrealistic "prey," such as a tuft of wool, as long as it is moving (Heil 1936; Drees 1952). When a spider detects a moving stimulus toward the side or rear, it turns, in either a large turn or a series of small turns, so that its body axis faces toward the stimulus. The spider often orients immediately to the stimulus (termed "fixation" by Land 1971). If the spider does not fixate, it may rotate again if the stimulus moves. After the spider fixates, it then seems to evaluate the stimulus and will either turn and run, court it, or attack it (reviewed in Land 1971). Both local motion (leg, head, and antennal movement) and global motion (movement of the entire body) by prey elicit attack in *Phidippus* jumping spiders (Bednarski et al. 2012). In addition, jumping spiders attend to shapes that hold particular relevance. For example, mosquito-eating spiders will attack abstract representations of prey, provided the abstract representations contain lines at the proper angles (Dolev and Nelson 2014). Spiders can use visual cues alone to distinguish prey from nonprey and among different types of prey (Edwards and Jackson 1993; Harland et al. 1999; Harland and Jackson 2000), assess the direction of movement and direct a predatory strike at the head of the prey (Bartos and Minias 2016), and avoid dangerous insects by sight (Nelson and Jackson 2006).

Vision is also used extensively in intraspecific communication. Courtship displays, like those observed by the Peckhams, have been described for dozens of species. Visual courtship elements may include waving of different pairs of outstretched legs, both together and in alternation; "knee pops" in which a bent leg is raised so that the patella is displayed to the female; sidling from side to side; palp waving;

and lifting and wagging of the abdomen. In many species, visual signals are accompanied by substrate-borne vibrations (e.g., Elias et al. 2012). Females assess courtship displays to identify males as conspecifics—especially important to males, which risk being attacked and eaten during courtship interactions—as well as evaluate the traits of prospective conspecific suitors. In several salticid groups, displays have rapidly diversified, as exemplified by isolated populations of *Habronattus pugilis* in the "sky islands" of southwestern mountaintops (e.g., Maddison and McMahon 2000; Masta and Maddison 2002; Hebets and Maddison 2005) and the speciose, tiny, colorful peacock spiders (Girard and Endler 2014; Girard et al. 2015; Girard et al. 2018). (A YouTube search for peacock spider displays yields results more gratifying than any verbal description could provide.) Jumping spiders also signal to conspecifics of the same sex. For example, contest dynamics between males are often largely mediated by vision (e.g., Taylor et al. 2001; Elias et al. 2008; Tedore and Johnsen 2015).

In spite of having sesame-seed-sized brains, jumping spiders are quite capable of cognitive tasks that often rely heavily on vision, such as vision-based learning and problem-solving (reviews in Cross and Jackson 2006; Jackson and Cross 2011; Jakob et al. 2011; Jakob and Long 2016; Aguilar-Arguello and Nelson 2021). To take just a few examples, spiders learn to avoid visual cues associated with aversive stimuli, such as shock, vibration, or heat (Drees 1952; Nakamura and Yamashita 2000; Bednarski et al. 2012; Long et al. 2015; Peckmezian and Taylor 2015b, 2017); avoid or locate food associated with particular colors or contextual stimuli (Skow and Jakob 2005; Jakob et al. 2007; Taylor et al. 2016; Vickers and Taylor 2018; Winsor et al. 2020); and solve a confinement problem (Jackson et al. 2001; Cross and Jackson 2015). Many species have been presented with variations of a detour problem, where a spider can see a goal but must follow an indirect path to reach it. Some salticids that are particularly good at solving this problem are from the genus *Portia*. These unusual salticids prefer to prey on other spiders, including stealthily stalking web-building spiders. To reach its prey, *Portia* may take elaborate detours, during which it may lose sight of its prey. Before embarking on its approach, *Portia* can select among complete and incomplete routes to the prey, examining a prospective detour path by visually tracing out routes from the target. If the potential route dead-ends, *Portia* will then look back at the target and begin again until it identifies a complete route (Tarsitano and Jackson 1994, 1997; Tarsitano 2006; Cross and Jackson 2019). Jumping spiders also use visual cues to select microhabitats to use as hunting and resting sites (de Omena and Romero 2010; Tedore and Johnsen 2016). Many salticids build silken retreats, to which they return at night or during inclement weather, and can learn the characteristics of prominent nearby features (beacons) to help them return to these retreats (Hoefler and Jakob 2006).

Jumping spiders do not attend to all incoming visual stimuli equally but selectively prioritize certain information in a process called visual attention (Dukas 2002). Visual attention is often categorized into two types. "Bottom-up" processes are driven by certain features of the stimulus itself. Similar to how we attend to movement in an otherwise static scene, spiders are more likely to attend to moving dots of particular sizes and speeds (Zurek et al. 2010; De Agrò et al. 2021). As in humans, spiders' attention to a visual stimulus wanes over time. Spiders habituate to repeated visual stimuli; evidence suggests that this visual decrement is a result of central nervous system (CNS) modulation rather than simple receptor fatigue (Humphrey et al. 2018; Humphrey et al. 2019; Melrose et al. 2019; Nelson et al. 2019). Also driving visual attention are "top-down," or goal-directed, processes. For example, in humans, experimental participants might be given instructions to look for a blue *x* among a field of letters of different colors and would focus their search accordingly. In spiders, individuals that are primed by a stimulus in another modality, such as the odor of conspecifics, are then more likely to detect an obscured visual stimulus of the same type (Cross and Jackson 2009, 2010; Carvell et al. 2017). Current work in one of our labs includes how cross-modal priming with sound or odor influences the gaze direction of the principal eyes. Many topics in visual attention that have been studied in humans, such as visual search, object recognition, and navigation, are now being addressed by studying the gaze direction of spiders (Winsor et al. 2021).

10.2.2 Modular Vision: Two Eye Types

The alert, responsive behavior of jumping spiders has naturally led to research on the visual system that underlies it. Jumping spiders have appealing faces that feature large forward-facing eyes, but those noticeable large eyes are only part of the story. Like other spiders, jumping spiders typically have four pairs of simple "camera-type" eyes, named for their relative positions on the cephalothorax, which provide a near-360° view of their surroundings (Fig. 10.1a). These eyes are of two types: the large principal eyes, also called the anterior median (AM) eyes, and three pairs of secondary eyes. While they are similar in external appearance, the principal and secondary eyes have distinct evolutionary histories, developmental pathways, internal structures, and neural connectivity to higher brain regions (reviewed in Morehouse et al. 2017).

10.2.2.1 Secondary Eyes of Jumping Spiders

Of the two eye types, the secondary eyes of jumping spiders have a simpler morphology than the principal eyes but are still impressively capable. The posterior lateral (PL) eyes and posterior median (PM) eyes are directed toward the side and rear of jumping spiders, while a pair of the forward-facing anterior lateral (AL) eyes share a field of view with the principal (AM) eyes (Fig. 10.1). The PM eyes are reduced or even absent in some species (Land 1985a).

The AL and PL eyes have large retinas and wide fields of view (Fig 10.1b) and serve as excellent motion detectors. When these eyes detect movement, a spider will turn to orient its forward-facing eyes toward the stimulus, even when other eyes are masked (Land 1971; Zurek and Nelson 2012a, b). While Land (1971) demonstrated

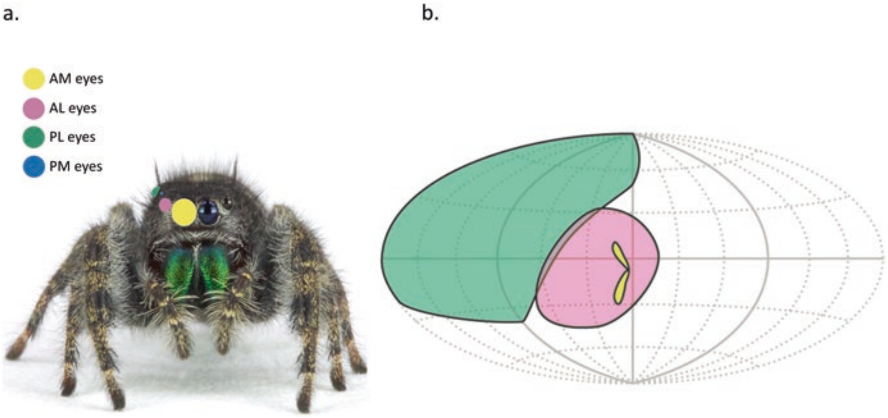

Fig. 10.1 Modular visual system of the jumping spider *Phidippus audax*. (**a**) The principal (AM) eyes are shown in yellow, while the secondary eyes are shown in reddish purple (AL eyes), bluish green (PL eyes), and blue (PM eyes). Reduced PM eyes are situated dorsally between the AL and PL eyes. (**b**) Orthographic projection mapping approximate visual fields of the AM eyes, AL eyes, and PL eyes of *Servaea incana*, a spider with similar eye size and arrangement to *P. audax*. The reduced PM eyes are not shown but view a small dorsal strip of overlap between the AL eyes and PL eyes. The point of origin is between the principal-eye retinas (i.e., figure corresponds to an anterior view of the spider's face). The principal-eye retina visual fields are boomerang shaped and overlap the AL-eye visual fields. The boomerang-shaped retinas can be moved. (Image recreated with permission from Morehouse 2020)

that salticids make orientation turns in response to stimulus movements of about 1°, which is close to the interreceptor angle of the PL eyes and was long considered to be the limit of motion detection, it has since been found that even smaller stimulus movements can be detected, a phenomenon known as motion hyperacuity (Zurek and Nelson 2012a). The AL eyes also appear to be responsible for detecting biological motion, the repetitive movement patterns characteristic of living organisms (De Agrò et al. 2021). Data suggest that, at least in some species, the AL and PL eyes have only a single peak in spectral sensitivity, making their vision monochromatic (Yamashita and Tateda 1976a; Terakita and Nagata 2014). The function of the PM eyes, much reduced or even missing in salticids, is unclear, and some authors have suggested that they are vestigial (Eakin and Brandenburger 1971). However, Terakita and Nagata (2014) point out that in *Hasarius adansoni*, the PM eyes express ultraviolet (UV) and blue-sensitive visual pigments and may therefore be specialized for detecting objects against the sky or changes in the brightness of the sky.

The photoreceptors in the secondary eyes have inverted rhabdomeres, which means that their photoreceptive segments lie below their cell bodies. Thus, light entering the inverted retinas of the secondary eyes must typically traverse the cell bodies before being absorbed in the rhabdomere. The result is lower light capture, compared to the principal eyes, due to scattering and inutile absorption by cell body constituents (Land 1985a), an effect partially ameliorated in some jumping spiders by the repositioning of the cell body to the side. The disadvantage of this latter approach is that it impacts the maximum acuity of these eyes by limiting the dense spatial packing of photoreceptors in the retinal mosaic (as both the photoreceptive segment and the cell body must be accommodated side by side for each receptor).

10.2.2.2 Principal Eyes of Jumping Spiders

In jumping spiders, the largest and most noticeable eyes are the principal eyes (anterior median (AM) eyes) (Fig. 10.1a), which have the highest spatial acuity of any animal with eyes of a similar size (reviewed in Harland et al. 2012). One might think that these large eyes have a correspondingly large retina that supports this acuity. However, jumping spider principal eyes have a tiny, boomerang-shaped retina (the visual field is shown in Fig. 10.1b). The extraordinary capabilities of these eyes result from a suite of interesting traits: eye tubes with a telescope-like structure, the ability to actively direct the eye tubes toward objects of interest independently of the spider's body movement, and a layered retina.

The basic structure of the principal eye is as follows. At the exterior end of each principal eye tube is a nonmoving converging corneal lens, part of the carapace, similar to that of the secondary eyes (Fig. 10.2). At the internal end of each eye tube, deep within the cephalothorax, is the boomerang-shaped retina. The eye's focal length, and thus its ability to resolve distant objects, is increased by a pit distal to the receptors. The pit's refractive index allows it to act as a diverging lens at the rear of the eye, magnifying the image received by the retinal cells and creating a Galilean telescope-like effect (Williams and McIntyre 1980; Blest and Price 1984).

The principal-eye retina has fewer than 1500 receptors (in contrast to the 200 million receptors in the human eye), and maximum spatial resolution is confined to a roughly 200-receptor region at the center of the boomerang. The field of view is correspondingly small (0.8–5° in the horizontal dimension, depending on species) (Blest and Price 1984). However, the disadvantages of a small retina size are partly overcome by six dedicated muscles that allow the eye tube to be rotated and moved horizontally and vertically inside the cephalothorax by as much as 50° (Fig. 10.2) (Land 1969a, b, 1971, 1972; Williams and McIntyre 1980; Blest et al. 1990). As the tube moves, it samples the larger image provided by the corneal lens, as if shining a flashlight at different parts of the image. These eyes thus provide excellent vision in a fraction of the space required by a spherical eye with similar capabilities (Land 1974; Harland and Jackson 2004), albeit sampling of the full visual field afforded by the corneal lens can only be accomplished through retinal movements, which take time.

Retinal movements vary depending on the stimulus that the spider is viewing. Land (1969b), using an ophthalmoscope, described four behaviors of the principal eyes: spontaneous movement across a scene; saccades, or rapid shifts to different parts of the scene; tracking a moving object; and scanning, or a back-and-forth horizontal motion accompanied by rotation as the spider inspects an object of interest (Fig. 10.3). Scanning seems to be unique to salticids and is certainly involved in

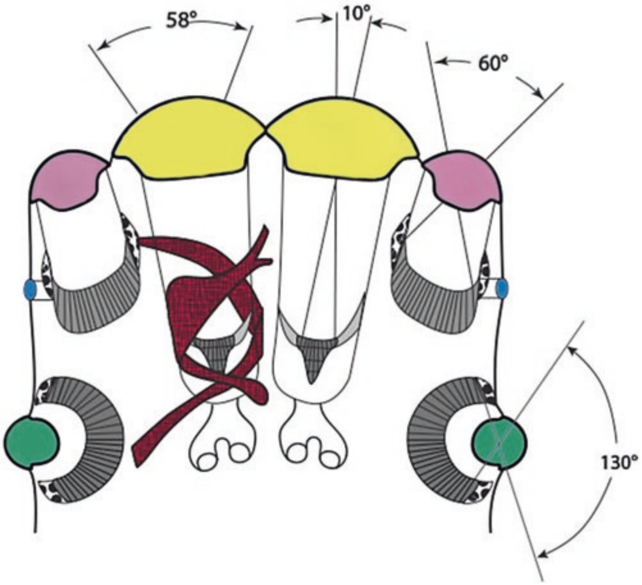

Fig. 10.2 A schematic horizontal section through the jumping spider head and eyes showing the internal structure of the visual system. The approximate fields of view for each eye pair are shown. The six muscles that control the principal eye tube are shown in dark red; the movements of the eye tube compensate for a small field of view. The moveable principal-eye retinas subtend about 10° of visual space at a given time within a maximum visual angle of about 58°. Retinas and their associated receptors are shown in dark gray. Cells containing pigment granules form a pseudo-iris outside the retina. Transparent vitreous cells (not shown) fill the space between the lens and retina. The optic nerve and first optic neuropil are shown for the principal eyes (see Sect. 10.3.6). (Image recreated with permission from Land 1969a)

object identification, as attested by the behavioral experiments described below. Land's findings have since been confirmed using a more advanced eye tracker developed over many years by an international team (Canavesi et al. 2011).

The retinal structure of the principal eyes is also complex. In contrast to the secondary eyes, the photoreceptors are everted (i.e., the photoreceptive segments are positioned toward incoming light, with the cell bodies below them), so light does not attenuate through the cell bodies and the receptors can be packed very closely (Blest 1985). Spatial acuity is greatest in the center of the boomerang, where the pit magnifies with minimal distortion closest to the optical axis and where receptors are more tightly organized. Acuity then falls off toward the boomerang tips (Blest and Price 1984). The central regions of the retina provide the highest known spatial acuity of any terrestrial invertebrate (Warrant and McIntyre 1993). For example, the principal eyes of the salticid *Portia* have spatial acuity greater than that of dragonflies, rivaling that of pigeons, and only a fifth that of humans (reviewed in Harland et al. 2012). Cells in the principal-eye retina are arranged in four tiers or layers. Layer I, furthest from the cornea, is specialized for resolving fine detail. It contains dense, tightly organized photoreceptors that function as light guides (Blest 1985;

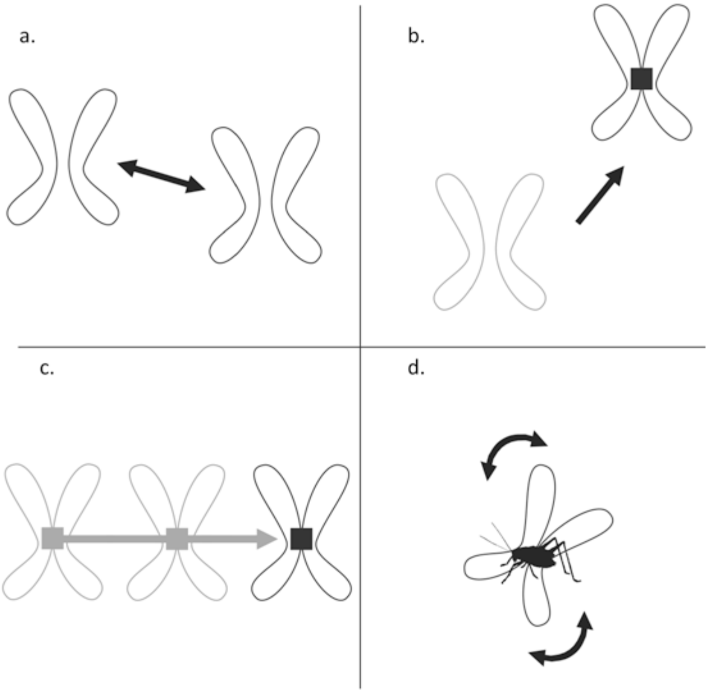

Fig. 10.3 The four categories of retinal movements: (**a**) exploratory movements, (**b**) saccades, (**c**) tracking, and (**d**) scanning. Double arrows represent back-and-forth movement, while single arrows represent movement in one direction. Opacity changes represent object displacement (lighter objects represent a starting position before displacement). Exploratory movements are spontaneous and can occur in any direction. The fields of view of the retinas converge when the spider is examining an object of interest. In the panel depicting scanning retinas, the cricket silhouette remains stationary, and the retinas exhibit torsional movements in either direction over it. (Image recreated with permission from Land 1969b)

Blest and Carter 1987; Blest et al. 1990; see Sect. 10.3.3.2). Layers II–IV have lower spatial acuity due to their larger, less densely packed photoreceptors, which allows greater passage of light to Layer I (Blest 1985). The tiered retina also helps solve an optical difficulty presented by the lens system. When light is transmitted through the pair of lenses, different wavelengths come into focus at slightly different distances behind the lens due to linear chromatic aberration. The best solution to this would be to position photoreceptors of different spectral sensitivities in the layers where the wavelengths they are maximally sensitive to are in best focus, and indeed, jumping spiders appear to do so, with short-wavelength-sensitive photoreceptors positioned in the distal two tiers (layers III and IV) and longer-wavelength-sensitive photoreceptors located in the proximal layers I and II (e.g., Nagata et al. 2012). In addition to this clever solution to chromatic aberration, the tiering of the principal eye retina provides another hidden benefit. Because the same region of space is sampled simultaneously by each tier, input from different tiers may be compared to extract color information without the loss in spatial acuity that typically accompanies color vision (reviewed in Harland et al. 2012; Morehouse 2020). Some jumping spiders have as many as four sensitivity peaks, ranging from UV to orange or red (Land 1969a; Yamashita and Tateda 1976a; Blest et al. 1981), sometimes augmented by intraretinal filters that shift the peak sensitivities of underlying photoreceptors (Zurek et al. 2015). In addition, evidence suggests that retinal tiering may allow spiders to estimate distance based on the relative degree of image defocusing on different layers (Nagata et al. 2012). Thus, these unusual eyes provide a moveable view of the world while supplying high acuity, color perception, and depth information.

10.2.2.3 Division of Labor in Jumping Spider Eyes

Beginning nearly a century ago, behavioral researchers masked different sets of eyes to deduce their functions and coordination. For example, spiders with secondary eyes masked failed to pivot toward a moving stimulus unless it was directly in front of their principal eyes (Homann 1928; Crane 1949; Land 1971). Those with only their principal eyes masked oriented to the stimulus but did not respond further. These results implied that the secondary eyes function as motion detectors and the moveable principal eyes are responsible for object identification. Forster (1979), using similar masking techniques, found that AL eyes are necessary for chasing prey, whereas principal-eye input is needed to initiate stalking behavior. Spiders made only short pounces onto prey when their secondary eyes were masked and required both principal and AL eyes to make long-range pounces. Spiders were less discriminatory when attacking faster-moving targets compared to slower-moving or stationary targets, suggesting that the principal eyes are primarily used to scan slower-moving or stationary targets. Later work showed that spiders back away from objects that appear to be looming closer; this behavior is driven by AL eyes, and the principal eyes are unnecessary (Spano et al. 2012). This result makes sense in light of the large field of view of the AL eye retina, which is necessary to detect the increasing subtended angle of the looming stimulus.

The AL eyes not only guide a spider's turning response to a stimulus but also guide the gaze direction of the moveable principal eyes. Using the updated eye tracker, we have documented that when the AL eyes are unmasked, the principal eyes effortlessly track moving stimuli; when the AL eyes are masked, the principal eyes are unable to locate suddenly appearing stimuli or track moving stimuli, although they can scan motionless images that appear directly in front of them (Jakob et al. 2018). Recent work confirms that jumping spiders can recognize stationary objects during an encounter (Rößler et al. 2021), a process likely mediated by the principal eyes.

The principal eyes do not automatically orient their gaze toward a stimulus detected only by the AL eyes (Bruce et al. 2021). If a spider is scanning a complex, biologically relevant image of a cricket with its principal eyes, it ignores a distractor oval appearing only in view of its AL eyes, but if it is scanning a less interesting oval, it does redirect its gaze toward the distractor. A spider examining a cricket image can, however, be distracted by a looming stimulus. This result is reminiscent of human visual behavior, when we are less likely to attend to a distractor appearing in our peripheral vision when we are examining closely a stimulus in our foveal vision (Savage et al. 2019).

10.2.3 Next Steps in the Study of Salticid Vision

We see at least two areas ripe for expanding research on salticid vision and visually guided behaviors. First, given the availability of new techniques, we expect that studies will increasingly incorporate both physiological and behavioral approaches rather than one or the other. This might include, for example, simultaneously recording neural and behavioral responses to visual stimuli to probe the neural underpinnings of visual cognition. Second, jumping spiders are an incredibly diverse family with over 600 genera and 6000 described species (World Spider Catalog 2022) and thus offer wonderful opportunities for comparative work. For example, both *Saitis barbipes* and *Habronattus pyrrithrix* are sexually dimorphic species, and males have red coloration. It would be tempting to conclude that the red color is a sexual signal, but Glenszczyk et al. (2022) found that *S. barbipes* lack long-wavelength-sensitive photoreceptors or spectral filters to perceive the color red. In contrast, the principal eyes of *H. pyrrithrix* have spectral filters that enable them to perceive longer wavelengths (Zurek et al. 2015). The retinal filters are confined to the center point of each retina, and using the eye tracker, we see that females direct them toward the center of the male display (D. Zurek, unpubl. data). This pair of studies illustrates the value of integrating physiology and behavior in a comparative context.

10.3 Distributed Visual Systems Across the Araneae

Beyond jumping spiders, there is enormous variety in the form that spider vision takes. This is perhaps unsurprising given that spiders are one of the world's most species-rich animal groups, with an estimated 80,000 extant species (Raven and Yeates 2007), of which only a little over half are described (nearly 50,000 species described to date; World Spider Catalog 2022). They are also an ancient lineage; the earliest spiders arose in the Devonian (Foelix 2011). Over the past 400 million years, these animals have evolved a remarkable array of lifestyles, behaviors, and ecological niches. Voracious predators as they are, they can be found in all of the world's major biomes and on every continent except Antarctica (Turnbull 1973). Although there are many reasons for the evolutionary success of spiders, their unique and remarkably elegant modular visual systems have certainly played a significant role.

10.3.1 Vision-Based Behavior Across Spiders

Visually guided behavior is widespread among spider families and is distributed across the phylogeny. We begin with a brief overview of the contexts in which different species use vision. Given that we surveyed many of the behaviors demonstrated by jumping spiders in the previous section, here we shift our emphasis to non-salticid species, though we periodically highlight salticids with unique traits and compare salticids with other groups.

Some spiders navigate using features of the environment such as visual landmarks and patterns of polarization. Similar to some jumping spiders, the Namib Desert spider *Leucorchestris arenicola* (family Sparassidae) uses visual beacons when navigating at night (Nørgaard et al. 2006), with nocturnal navigation being essential to avoid oppressively high daytime temperatures. The wolf spider *Lycosa tarentula* (family Lycosidae) requires visual input for path integration when homing (Ortega-Escobar 2002). The ground spider *Drassodes cupreus* (family Gnaphosidae) uses polarized light from the sky to navigate home after bouts of foraging (Dacke et al. 1999).

Spiders also visually assess their environment to increase the chance of capturing prey. For example, the nocturnal orb-web spider *Larinioides sclopetarius* (family Araneidae) builds its web near artificial lights where prey is more abundant. Spiders are not simply responding to the presence of prey; in the lab, naïve spiders sought out better-lit spots without the confound of prey (Heiling 1999). The orb-weaver *Nephila clavipes* (family Araneidae) spins webs of different spectral qualities depending on the properties of ambient light, such as brightness and wavelength composition, and the webs are thus harder for prey to see (Craig et al. 1996). The spider-eating specialist salticid *Portia labiata* exploits UV-reflecting silk stabilimenta in the webs of other spiders to locate them (Li and Lim 2005).

Other than for navigation and selecting foraging sites, many taxa use vision for prey capture. Arboreal green lynx spiders *Peucetia viridans* (family Oxyopidae) spend their daylight hours stalking prey that reside on the branches of plants, pouncing from the vantage point of a higher branch (Whitcomb and Eason 1965). Another cursorial hunter, *Tibellus macellus* (family: Philodromidae), uses its vision to capture a wide variety of small insect prey (Huseynov 2008). The crab spider *Misumena* (family Thomisidae) waits on flowers for arriving prey; it is so reliant on motion cues that it sometimes walks right over stationary prey (Morse 2007). The net-casting spiders (family Deinopidae) hold a small silken snare between their front legs and use enormous eyes, sensitive in dim light, to help them quickly scoop up prey (Robinson and Robinson 1971; Stafstrom and Hebets 2016).

Spiders have many predators, notably birds, wasps, and other spiders, including conspecifics, and have evolved many visually guided antipredator strategies (reviewed in Robledo-Ospina and Rao 2022). Crab spiders perch on a flower, ready to grab an unsuspecting pollinator, and some can select floral background colors that best complement their own (Heiling et al. 2005), a process presumably mediated by their visual system (Defrize et al. 2011). The ambulatory wolf spider

Schizocosa ocreata instead flees when a simulated bird shadow passes overhead (Lohrey et al. 2009).

Vision can also be used to assess mates during elaborate courtship displays and competitors during agonistic social encounters. For example, wolf spiders rely on vision during conspecific interactions (Rovner 1996). Extravagant visual displays have been thoroughly explored in wolf spiders of the genus *Schizocosa*: males display foreleg ornamentation to females during courtship, which improves mating success in some species (e.g., Hebets and Uetz 1999). As noted earlier, elaborate courtship displays involving color, pattern, and motion are widespread in jumping spiders as well, including the paradise spiders of North America (genus *Habronattus*, Elias et al. 2012) and the peacock spiders of Australia (genus *Maratus*, Girard et al. 2015). Fighting with a competitor can be costly, so mutual visual assessment of fighting ability can allow spiders to settle disputes unscathed. Many spiders assume a defensive posture by lifting their first pair of legs when visually presented with a conspecific competitor, which can be used for rank assessment (Riechert 1982). By eavesdropping on competing males, female *Thiania bhamoensis* jumping spiders show changes in preference between two potential mates (see Chan et al. 2008).

While many spiders rely on vision, it is worth noting that many of the visual cues described above are accompanied by signals and cues in other modalities. This multimodality is important to consider in the context of visual system evolution because it informs both neural integration of visual inputs and resulting behavioral responses. The most common is mechanoreception, the ability to detect vibrations. The strikingly diverse web-building spiders rely on vibratory cues from prey entangled in webs (e.g., Landolfa and Barth 1996). Other examples include *Cupiennius salei* (family Trechaleidae; this species is well represented in the literature but recently moved from Ctenidae; see Piacentini and Ramírez 2019), which, while it uses some visual cues, relies primarily on vibratory cues for localizing prey (reviewed in Barth 2002; Fenk et al. 2010), and fishing spiders of the genus *Dolomedes* (family Pisauridae), which detect vibrations borne on the water's surface (Bleckmann and Rovner 1984). Furthermore, many spiders rely on chemoreception mediated by receptors on their appendages (e.g., Tietjen and Rovner 1982; Persons and Uetz 1996; Foelix 2011). Other modalities, such as audition, are also important (Shamble et al. 2016; Stafstrom et al. 2020; Zhou et al. 2022). How different spider lineages have evolved to prioritize inputs from these various senses or integrate them with vision is an area ripe for deeper investigation, especially considering that many (but not all) groups that heavily rely on other senses exhibit reduced visual systems.

10.3.2 Origin and Evolution of Spider Eyes

Arachnids are among the few groups of arthropods that rely primarily on single-lens eyes (Land 1985a). Most other arthropods, including insects and crustaceans, use a pair of compound eyes as their primary visual organs (although the role of ocelli should not be understated; see Chap. 8 in this volume). Single-lens eyes can potentially support better resolution for eyes of their size (Land 1981; Land and Nilsson 2012; Nilsson 2021). Non-spider arachnids vary in eye types and number, but vision is reported to be relatively poor in many of these animals. For example, scorpions (Arachnida: Scorpiones) and whip spiders (Arachnida: Amblypygi), like many other arachnids, have two morphologically distinct eye types (Bedini 1967; Loria and Prendini 2014; Lehmann and Melzer 2018a; Sinakevitch et al. 2021), but it appears that other sensory modalities are more important (Miether and Dunlop 2016). Among the arachnids, spiders have undoubtedly evolved the greatest visual system diversity (Strausfeld 2012). In spiders, many lineages have poor vision (even lacking eyes altogether), while others have exceptional vision (e.g., the Salticidae and Deinopidae).

10.3.2.1 Origin and Development

As described in Sect. 10.2.2 for salticids, other spider families also have four pairs of eyes divided into two types (the principal and secondary eyes, Homann 1928), with specific eye pairs named for their anatomical position on the cephalothorax. Historically, the delineation between principal and secondary eyes was contingent on whether their retinula cells are everted (principal eyes) or inverted (secondary eyes). Unlike the principal eyes, the secondary eyes often possess a light-reflecting tapetum (see Sect. 10.3.3.4) and do not have muscles for movement (see Sect. 10.3.5.1). The two eye types also have different neural connectivity and patterns of development (Strausfeld and Barth 1993; Strausfeld et al. 1993). In spite of their name, the principal (AM) eyes are not always the primary visual organ for spiders; in some spider lineages, it is one of the secondary eye pairs (AL, PM, or PL) that is most prominent. These eye types also have different evolutionary histories (Morehouse et al. 2017). Here, we provide a brief overview.

The ancient Cambrian relatives of spiders likely had both single-lens and compound eyes (Paulus 1979). Fossil evidence supports this, including those of trilobites and horseshoe crabs, which possess single-lens “medial” and compound “lateral” eyes (Paulus 2000; Strausfeld et al. 2016; Lan et al. 2021). The medial eyes are evolutionarily related to the lateral eyes and might have derived from an ancestral visual organ before the diversification of arthropods (Zhou et al. 2016). Genetic evidence suggests that key mechanisms of eye development are mediated by ancient, deeply conserved gene regulatory networks (reviews in Friedrich 2006; Morehouse et al. 2017). The ancestral single-lens eye is thought to be homologous with the principal eyes of spiders, medial eyes of other arachnids, and ocelli of insects, while the ancestral compound eye is thought to be homologous with the secondary eyes of spiders, lateral eyes of other arachnids, and modern compound eyes of insects. The secondary eyes of spiders might have arisen from the subdivision and subsequent fusion of ommatidia from an ancestral compound eye or the enlargement of its individual ommatidia (e.g., Buschbeck 2014). How chelicerate eyes evolved has not been resolved, so it is unclear if this occurred once or multiple times in spiders and other arachnid lineages (Miether and Dunlop 2016), but it seems that gene duplication has played an important role in their visual system evolution (Gainett et al. 2020).

The principal and secondary eyes of spiders develop from separate areas of the ectoderm of the head: a median ectodermal groove and the lateral head ectoderm, respectively (Schomburg et al. 2015). During development, the principal eyes innervate the protocerebrum, and the secondary eyes innervate the lateral protocerebrum (Strausfeld and Barth 1993; Strausfeld et al. 1993). The principal eyes derive from their own progenitor cells, much like the ocelli of insects, and a bilateral pair of "eye-fields" fragment in a cluster to form the secondary eyes, much like the compound eyes of insects (Schomburg et al. 2015; Samadi et al. 2015). The development of eyes in *Drosophila melanogaster* is dictated by a core set of developmental genes—including sine oculis (*so*), eyes absent (*eya*), dachshund (*dac*), atonal (*ato*), and orthodenticle (*otd*)—and two Pax6 orthologs, which determine the eye field during early development—eyeless (*ey*) and twin of eyeless (*toy*)—all of which are found across arthropods (reviewed in Friedrich 2006; Morehouse et al. 2017). In insects, these retinal determination network genes regulate ocelli and compound eye development. In spiders, each eye type expresses a unique combination of these transcription factors (Schomburg et al. 2015; Samadi et al. 2015; Baudouin-Gonzalez et al. 2022).

Some conserved genes in spiders appear to serve similar functions as in insects or vertebrates, while important differences have been noted in others. For example, the *Drosophila* proneural gene *ato* is present in spiders (Samadi et al. 2015; Baudouin-Gonzalez et al. 2022). In both *Drosophila* and spiders, *ato* seems to initiate photoreceptor differentiation (Baudouin-Gonzalez et al. 2022). Recently, Baudouin-Gonzalez et al. (2022) found that similarly to vertebrates, Wnt signaling and potentially the gene hedgehog (*hh*) in spiders may restrict the expression of retinal determination genes around each eye primordium, providing a plausible mechanism underlying variation in eye number, placement, and size. In contrast, the expression of the ubiquitous eye development master control gene Pax6 does not seem to be expressed during eye development in the common house spider *Parasteatoda tepidariorum* (family: Theridiidae) (Schomburg et al. 2015; Baudouin-Gonzalez et al. 2022) or several other genera investigated so far (e.g., *Acanthoscurria*, *Pholcus*, *Marpissa*; L. Baudouin-Gonzalez and L. Sumner-Rooney, pers. comm.). However, Samadi et al. (2015) found late-stage expression of Pax6 in the principal eyes of *C. salei*. Recent work has shown that instead of Pax6, an ortholog of a different Pax gene called Pax2 is expressed in the spider secondary eye primordia (Janeschik et al. 2022). Thus, variation in spider eye arrangements seems to involve network components that are common to insects or vertebrates and others that are unique. Future work is needed to better understand the extent to which these ancient gene networks show conserved functions and how gene duplication and subsequent functional divergence impact spider eye development. Another interesting future direction is how the visual system function changes across later ontogenetic stages. For example, Goté et al. (2019) found that in jumping spiders, the smaller eyes of juveniles are likely less sensitive than those of adults but still benefit from high visual acuity.

10.3.2.2 Eye Arrangement and Visual Fields

When beginning to identify spiders, a novice first learns that families can be distinguished by the size and positions of their eyes (Fig. 10.4; Foelix 2011). For example, many visual hunters that stalk and pounce on prey, including jumping spiders and wolf spiders (family Lycosidae), exhibit forward-facing eyes with a prominent pair (AM and PM eyes, respectively). There are exceptions, however, such as the nursery web spiders (family Pisauridae), which are also active hunters but have equally sized eyes. The night-active net-casting spiders (family Deinopidae), which seize passing prey with a small web stretched between their legs, have an enormous pair of PM eyes and see exceptionally well in dim light. In fact, the PM eye of *Deinopis subrufa* is among the largest simple eyes of all arthropods, with a diameter exceeding 1 mm (Blest and Land 1977). The ambush-hunting crab spiders (family Thomisidae) have similarly sized eyes relative to one another—with slightly enlarged AL eyes—which are well distributed around the cephalothorax. The

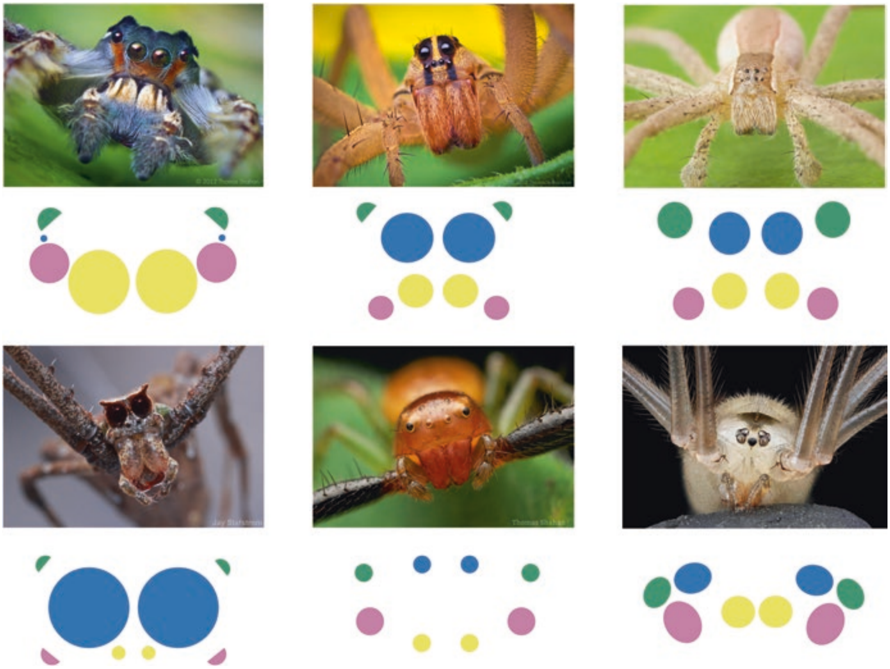

Fig. 10.4 Typical spider eye patterns used for family identification. Starting in the upper left corner, from left to right, each row in turn: Salticidae (*Phidippus putnami*), Lycosidae (*Rabidosa rabida*), Pisauridae (*Pisaurina mira*), Deinopidae (*Deinopis aurita*), Thomisidae (*Synema parvulum*), and Pholcidae (*Pholcus phalangioides*). Principal (AM) eyes are shown in yellow, while the secondary eyes are shown in reddish purple (AL eyes), blue (PM eyes), and bluish green (PL eyes). (Images courtesy of Thomas Shahan (Salticidae, Lycosidae, Thomisidae), Jay Stafstrom (Deinopidae), and the USGS Bee Inventory and Monitoring Lab (Pholcidae))

web-building cellar spiders (family Pholcidae) have clusters of diminutive eyes. Exceptions to these family-level characteristics occur in genera and species with specialized lifestyles.

With the visual fields of the principal and secondary eyes combined, most spiders can see nearly 360°, but this is certainly not universal. The extent to which a spider can see the full hemisphere surrounding it is determined by the location of the eyes on the cephalothorax, which direction the eyes are facing, and their fields of view (FOV) or the solid angle of space outside of the animal that is imaged by the retina. The FOV of each eye is contingent on its size, the focal length of its lens, and the dimensions and position of the retina. The FOV can be calculated or measured using ophthalmoscopic techniques (e.g., Homann 1928; Land 1985b; Land and Barth 1992; Goté et al. 2019). The FOV size and shape are highly variable within and across species, even for a corresponding eye type. For instance, the principal eyes of crab spiders have a larger FOV than those of jumping spiders (Insausti et al. 2012).

Two transverse rows of similarly sized eyes are found in many spider families (Fig. 10.4; Homann 1971; Land 1985a). The bottom row is slightly recurved and comprised of the centrally located principal eyes flanked by the AL eyes, while the top row is slightly procurved and comprised of the PM and PL eyes. This pattern was hypothesized by Homann (1971) as the primitive state for spiders. Recent work across arachnids suggests that secondary eyes are usually in bilaterally symmetric triads in basal groups, while the principal eyes assume a central position (Miether and Dunlop 2016). In spiders, the secondary eye triads intermingle with the principal eyes to yield two basic ground patterns: either all eyes clustered together on a single tubercle (raised area), as usually seen in the Mygalomorphae, or eyes positioned in two rows, as often seen in the Araneomorphae (Fig. 10.5). Variation in these ground patterns is apparent across the phylogeny (Fig. 10.5). The presumed basal two-row eye pattern of araneomorphs is supported by recent molecular phylogenetic and unipartite directional network approaches. Within the speciose retrolateral tibial apophysis (RTA) clade (i.e., mostly ground-dwelling araneomorph spiders that are synapomorphic for a tibial projection on the pedipalps of males), the two-row pattern was supported as the ancestral state; the Ctenidae configuration (Fig. 10.5) independently evolved seven times, while the *Agelenopsis*, Oxyopidae, Lycosidae, Selenopidae, and Salticidae patterns (Fig. 10.5) each evolved once Hazzi and Hormiga 2022. Genes that determine the location and size of eyes may be conserved but differ in spatial or temporal expression patterns (Morehouse et al. 2017).

Fig. 10.5 (continued) Catalog 2022), shown are 40 that were selected for their reliance on vision, phylogenetic position, or within-family diversity. Note that *Cupiennius*, a genus well represented in the spider vision literature, was recently moved from Ctenidae to Trechaleidae. The visual abilities of the Deinopidae, Sparassidae, Oxyopidae, Pisauridae, Lycosidae, Thomisidae, Philodromidae, and Salticidae also have been relatively well studied (all of which are in the RTA clade, except the Deinopidae). Families that rely on vision to hunt often have enlarged eye pairs. Field guides and taxonomic keys (Ubick et al. 2005; Elliott 2006; Platnick 2020) were used to determine the most common eye pattern for each family

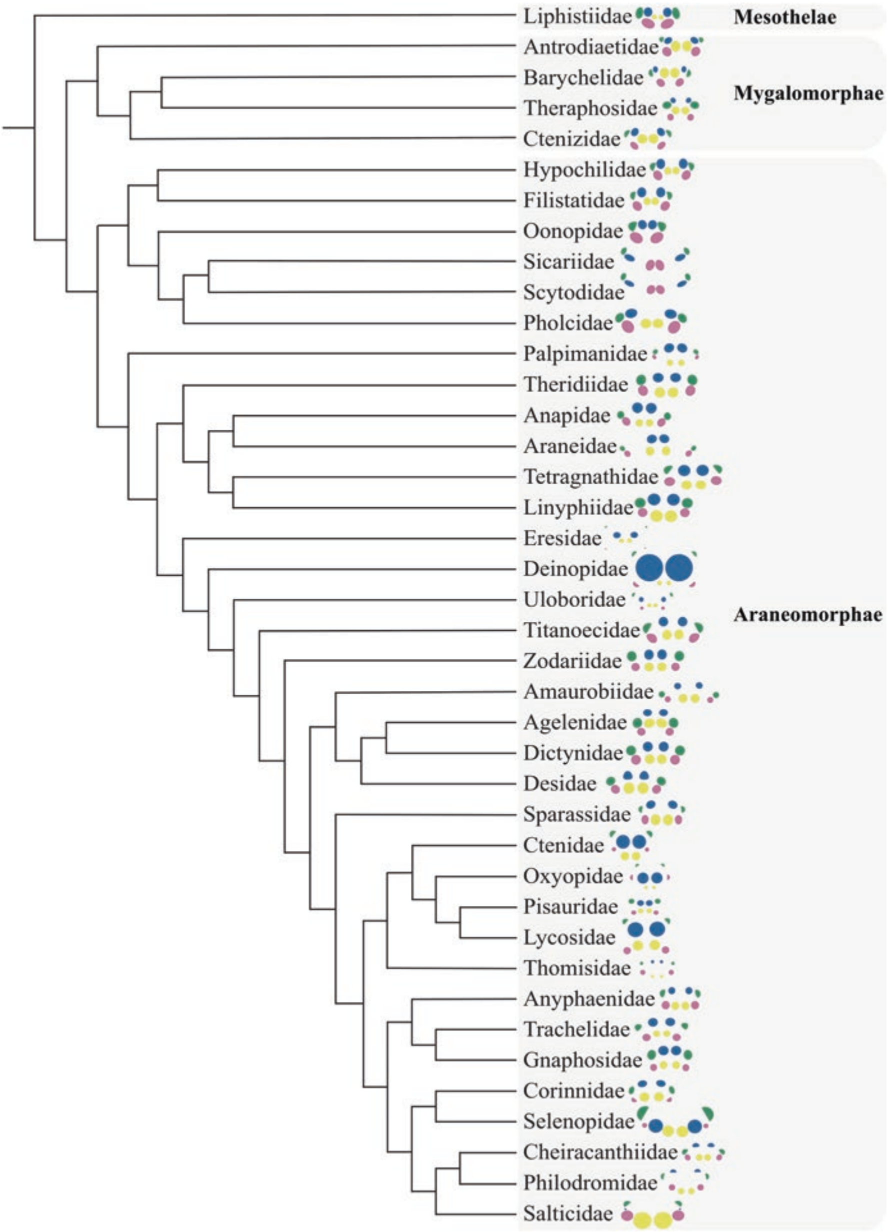

Fig. 10.5 Phylogeny with typical eye patterns for each family mapped. Tree topology inferred from Wheeler et al. (2017), with branch lengths not to scale. Principal (AM) eyes are shown in yellow, while the secondary eyes are shown in reddish purple (AL eyes), blue (PM eyes), and bluish green (PL eyes). Families are grouped in the suborder Mesothelae (which contains a single extant family) or Opisthothelae, the latter of which is subdivided into the infraorders Mygalomorphae (31 families) and Araneomorphae (99 families). Of the 131 currently valid families (World Spider

(continued)

Additional molecular genetic approaches will likely provide insights into the evolution of these eye patterns.

The maintenance of complex sensory systems is energetically expensive, particularly for vision (Niven and Laughlin 2008); if the cost of maintaining eyes begins to outweigh the benefits of their use (e.g., due to changes in ecological niche), we would expect evolutionary loss. In the Dysderidae, Oonopidae, Sicariidae, and Scytodidae, the principal eyes are absent (Land 1985a; Morehouse et al. 2017; Fig. 10.5). Some spiders have even fewer eyes (e.g., Caponiidae has representatives with one and two pairs), and others, like the Laotian-cave-dwelling huntsman spider *Sinopoda scurion* (family Sparassidae), have no eyes (Jäger 2012). Within the family Uloboridae (Fig. 10.5), some species spin simple webs and have reduced visual demands, while others have larger and more complex webs. These spiders show losses and rearrangements of eyes in accordance with web reduction (Opell and Cushing 1986; Opell and Ware 1987; Opell 1988). For example, many uloborids that operate single-line reduced webs also show losses of both anterior eye pairs (e.g., *Miagrammopes* spp.), but they still require enough visual coverage to operate their webs. To compensate for eye loss, optical tubercles shift the PL-eye visual fields ventrally, retinal position and their symmetry change, and curvature of the lenses can change to further expand visual angles (Opell and Cushing 1986). Their expanded visual fields show similar overall coverage compared to species with a full complement of eyes (e.g., *Octonoba sinensis*), but spiders with fewer eyes likely expend less energy for eye development and maintenance. Uloborids that build triangle webs, such as *Hyptiotes cavatus*, appear to have six functional eyes because their vestigial AL eyes lack retinal cells (Opell and Ware 1987). In these spiders, increases in resolution (see Sect. 10.3.3.2) might also help compensate for eye loss (Opell 1988). In uloborids with complex orb webs and a full complement of eyes (e.g., *Uloborus glomosus*), the visual fields have overlapping patterns that might help with localizing prey approaching from different orientations (Opell and Ware 1987). Among the species investigated so far, visual system changes were not necessarily progressive; rather, they may have been independent adaptations (B. Opell, pers. comm.). In many cases, eye placement and their associated visual fields can be correlated with present-day function. For example, front-facing eyes assist cursorial spiders with prey capture (Forster 1979), and dorsally placed eyes with greater fields of view might help with aerial predator detection (Opell and Ware 1987). Eye masking experiments will be useful for ascertaining the behavioral functions of different eye pairs.

10.3.3 Structure and Optical Performance of Eyes

Spider eye anatomy was first described by pioneers such as Grenacher (1879), Bertkau (1886), Hentschel (1899), Widmann (1907,1908), and Scheuring (1913, 1914). Deeper investigations into the physiology and optics of spider eyes were later undertaken in the Lycosidae (Homann 1931; Bacetti and Bedini 1964), Thomisidae (Homann 1934), and Pisauridae (Williams 1979). The eyes of many spider families were described by the renowned German arachnologist Heinrich Homann (e.g., Homann 1951, 1952, 1971; reviewed in Levi 1994). Starting in the late twentieth century, a collection of influential papers on spider eyes was published by David Blest and Michael Land (e.g., Blest and Land 1977). Detailed studies of the tiger wandering spider *Cupiennius salei* by Friedrich Barth, Axel Schmid, and colleagues (e.g., Land and Barth 1992; Schmid 1998) included not only the visual system but other sensory systems as well. Recently, there has been a resurgence of interest in comparative spider vision in a number of labs around the world.

The optical power of eyes determines their maximal potential performance, but realized performance depends on other factors, such as ambient light conditions, the ability of the retina to sample an image, and how the nervous system processes incoming information. Assessing the optics of animal eyes requires a combination of mathematical modeling and careful experimentation, the details of which are beyond the scope of this chapter. Here, we provide a cursory overview of spider eye optics, with an emphasis on resolution and sensitivity (for in-depth reviews, see Warrant and McIntyre 1993; Land 1985a; Land and Nilsson 2012; Cronin et al. 2014; Meece et al. 2021).

10.3.3.1 Corneal Lens Properties

The refractive properties of the corneal lens in combination with retinal placement determines how objects are focused on the retina. This varies both across species and between different eyes of the same individual. The first useful metric is focal length, which is defined as the distance from the nodal point of a lens to the point where light rays form a focused image (the focal point, Land and Nilsson 2012). Focal length is determined by the radius of curvature and the refractive power of the lens and can be measured using Homann's hanging drop technique (Homann 1928). The longest known focal length in spiders belongs to the principal eyes of the salticid *Portia fimbriata* and is 1.980 mm (without the pit lens, it would be 1.701 mm; Williams and McIntyre 1980). In contrast, the focal length of the PM eyes of the trechaleid *Cupiennius salei* is around 0.448 mm (Land and Barth 1992), and those of many web-building species are shorter still. While longer focal lengths are useful for greater magnification, they can increase the extent of chromatic aberrations, resulting in blurring when light rays of different wavelengths are not brought to a single focus. As discussed previously, the pit lens in the principal eyes of salticids provides a telephoto component (Williams and McIntyre 1980), but it also magnifies chromatic aberrations, which may be compensated for by retinal tiering (Land 1969a). Spherical aberration, another instance in which all light rays are not brought to a single focus, can occur in lenses with larger apertures and relatively shorter focal lengths. As another example of evolutionary corrective optics, spherical aberration is nearly eliminated in the PM eyes of *Deinopis* because of a precise gradient of refractive indices in their lens (from the center to the edges; Blest and Land 1977). Similar gradient-index optics are found in jumping spider principal eye lenses as well (Williams and McIntyre 1980), suggesting that this clever solution to spherical aberration may be widespread across spiders.

The minimum focusing distance is the nearest distance between an external object and the point at which light rays form a focused image on the retina. This can be calculated using focal length, lens diameter, and photoreceptor spacing (Land 1981), which also vary across species and eye pairs. For example, the principal eyes of *P. fimbriata* have a minimum focusing distance of about 20 cm (Williams and McIntyre 1980), while the principal eyes of *C. salei* have a minimum focusing distance of about 4 mm (Land and Barth 1992). Different eyes of the same animal usually have different focusing distances, which influences the behavioral utility of each eye pair. For example, in Lycosidae, anterior eyes are optimized for viewing close objects, while posterior eyes are focused further away. The principal (AM) eyes of *Lycosa leuckarti* have a minimum focusing distance of 4.5 mm, and the AL eyes have a minimum focusing distance of 2.7 mm (Clemente et al. 2010). Given how small these distances are, most close-range objects that the spider might encounter should be in focus. In contrast, the PL eyes of *L. leuckarti* have a minimum focusing distance of 24 mm, and the PM eyes have a focusing distance of 32 mm (Clemente et al. 2010). In these eye pairs, more distant objects will be in focus. Eyes that focus on close objects might facilitate prey capture and intraspecific communication, while eyes that only focus on objects several body lengths away might be better suited for long-distance detection and identification.

In addition to these focusing functions of lenses, the transmission properties of the cornea can influence wavelength sensitivity. For example, because UV light is not filtered out by the cornea in many visually hunting families, UV light perception is possible. However, spiders in dim environments, such as those from the families Atypidae and Ctenizidae (Fig. 10.5), often have corneas that block much of the incoming UV light, while species inhabiting open (i.e., not forested) areas often have UV-transmitting corneas (Hu et al. 2014). These differences may contribute to the use of UV light in a number of contexts, including communicatory behaviors. For example, the corneas of all investigated jumping spiders transmit at least some UV light above 290 nm (Hu et al. 2012), and some species attend to UV signals during sexual signaling (Li et al. 2008).

10.3.3.2 Resolution

Spatial acuity, or the ability to resolve fine details, varies across species and across eyes within individuals. For high-resolution vision (of static objects; see Sect. 10.2.2.1 for an explanation of motion hyperacuity), adjacent points in space must be resolved independently by different receptors (reviewed in Meece et al. 2021). Resolution depends on rhabdom density (see Sect. 10.3.4) and their associated interreceptor angles (denoted as $\Delta\Phi$), which can be calculated by dividing the space between the center of adjacent receptors by the focal length (Land 1985a). A smaller $\Delta\Phi$ often correlates with a smaller acceptance angle ($\Delta\rho$), which describes the maximum angle at which incident light can enter the receptor. Narrower interreceptor and acceptance angles confer better resolution vision at the expense of reduced light capture. These metrics can be used to quantify differences between species. Most spiders have an ΔΦ of 1–5° across both eye types (Land 1985a). However, visually hunting lineages often exhibit higher resolution at least in a subset of their eyes. For example, huntsman spiders of the genus *Olios* (family Sparassidae) have an ΔΦ of 1.8 in their AL eye (Land 1985a). The Salticidae have an unusually small ΔΦ of 0.04–0.13° in the center of their principal eyes and a correspondingly narrow Δρ (0.15° for the typical salticid *Phidippus johnsoni*) (Land 1981). The secondary eyes of salticids have larger interreceptor and acceptance angles than the principal eyes (e.g., the AL eyes of *P. johnsoni* have an ΔΦ of 0.5–1.5°; Land 1969a). While the principal eyes are often used to inspect objects, the spatial acuity of the secondary eyes can exceed that of the principal eyes in some cases. For example, the principal (AM) eyes of *Cupiennius salei* have an ΔΦ of 2.9° and an Δρ of 5.4°, while the large PM eyes have an ΔΦ of 1.0° and an Δρ of 2.0° (Land and Barth 1992; Grusch et al. 1997; Pirhofer-Walzl et al. 2007). Similarly, the principal (AM) eyes of ground crab spiders of the genus *Xysticus* have an ΔΦ of 3.6°, while the slightly enlarged AL eyes have an ΔΦ of 1.8–2.6° (Homann 1934; Land 1985a).

Some spider groups have evolved adaptations to increase the resolution of their everted principal eye photoreceptors. For example, the Salticidae have evolved narrower and more densely packed photoreceptors in their principal-eye retinas (although there is variation; see Blest et al. 1990). The physical isolation of rhabdomeres also improves resolution, as in the Oxyopidae, compared to the closely related Pisauridae (Fig. 10.5), which have contiguous rhabdomeres of adjacent receptors (Blest 1985). Resolution can be improved further with receptor pigment shielding, which absorbs stray light, neatly exemplified by the secondary eyes across much of the Salticidae (e.g., Cerveira et al. 2021). The light capture of photoreceptors can be enhanced when each rhabdomere is surrounded with material that has a lower refractive index (i.e., is less optically dense), which traps light by internal reflection (reviewed in Warrant and McIntyre 1993). This functions similarly to a fiber optic cable. A possible example is the salticid *Portia*, which lacks some organelles and other cellular components, such as microtubules in the cytoplasm of the receptors in the acute regions of their retinas, perhaps to increase the refractive index difference between each rhabdomere and its surroundings (Blest and Price 1984). While it appears that the morphology of rhabdoms is more conserved in comparison to dioptric structures, rapid modifications have occurred in some groups, such as the salticids, which is potentially related to their diversification. We recommend that readers consult Blest (1985) for a more comprehensive review of spider photoreceptor ultrastructure.

10.3.3.3 Sensitivity

Sensitivity, or the ability to capture light, also varies across species and across eyes within individuals. For low-light vision, nocturnal and crepuscular spiders must make the greatest use of relatively few photons available (reviewed in Meece et al.

2021), whereas diurnal species often show lower visual sensitivity, relying instead on light available during their active period. Sensitivity is influenced by the F-number, which divides the focal length by the aperture and describes the physical light-gathering ability of an eye. A lower F-number corresponds to a shorter focal length or wider aperture and optically confers higher sensitivity (Warrant and McIntyre 1993). For example, nocturnal net-casting spiders of the genus *Deinopis* have an F-number of 0.58 in their PM eyes (Blest and Land 1977), the nocturnal wolf spider *Arctosa variana* has an F-number of about 1 in their PM eyes (Land and Nilsson 2012), and the diurnal jumping spider *Portia fimbriata* has an F-number of 2.4 in their principal (AM) eyes (Warrant and McIntyre 1993). To measure sensitivity, the S-number can be used, which is a product of the relative aperture of the eye, the cross-sectional area of the receptor, and the proportion of light entering a receptor that is absorbed (Land 1985a). A higher S-number indicates a more sensitive eye; for example, the PM eyes of *Deinopis* have an extremely high S number of 101, while the principal eyes of *Phidippus* have a much smaller S-number of 0.04 (Land and Nilsson 2012). The proportion of light that is actually absorbed by a receptor depends on the dimensions of the photoreceptive segment, the segment's light-guiding properties, and the amount of visual pigment and can be nearly doubled through the presence of a light-reflecting tapetum (see Sect. 10.3.3.4). At the physiological level, sensitivity can also be estimated using electroretinogram (ERG) or intracellular recordings in response to light (e.g., Yamashita and Tateda 1976b; Laughlin et al. 1980; Barth et al. 1993; Yamashita and Nakamura 1999).

Some spider groups have evolved adaptations to increase the sensitivity of their inverted secondary eye photoreceptors. For example, convergently in the Sparassidae and Salticidae (Fig. 10.5), cell bodies of the secondary eye photoreceptors have shifted laterally, moving them out of the light path of the rhabdomeres (Homann 1971; Eakin and Brandenburger 1971; Blest 1985; Morehouse 2020). This shift, however, necessarily increases the distance between neighboring photoreceptors, resulting in reductions in visual acuity. In other spider families, the photoreceptor cell bodies have become more transparent, although the effect of these changes on cell physiology is not understood (Morehouse 2020). Many spider species have also increased the width of their secondary eye rhabdomeres to increase sensitivity, again an adaptation that typically comes at a cost to visual acuity. Other spider species increase visual sensitivity by pairing rhabdomeres (even interdigitating microvilli) or reducing pigment granules (shielding) between units, which allows for optical pooling (Cerveira et al. 2021). Microvilli contained within the rhabdomeres can also change size during circadian cycles, allowing for light- and dark-adapted states (Uehara et al. 1993). In some other arthropods, screening pigments in visual cells can migrate in response to light and dark cycles, but this does not appear to happen in the supporting glial cells of spiders to an appreciable extent (Blest 1985). Although jumping spiders are particularly known for their diurnal activity, some species hunt under poor light conditions; for example, *Cyrba algerina* spiders have several adaptations to increase sensitivity, which presumably help them find prey in dark crevices (Cerveira et al. 2021). Thus, improving sensitivity can also be important for some day-active spiders.

10.3.3.4 Secondary Eye Tapeta

The tapetum is a reflective mirror-like layer of material composed of guanine crystals at the base of the retina that returns unabsorbed photons to the rhabdomeres for a second chance at capture, thereby effectively increasing photoreceptor sensitivity. While principal eyes universally lack tapeta, many spider families have tapeta in their secondary eyes. Different types of tapeta have been described in spiders, such as the "primitive" tapetum (which forms a single layer perforated by the passage of retinula axons) of the Theraphosidae and other mygalomorphs, the canoe-shaped tapetum of the Sicariidae and Theridiidae, and the elaborate grate-shaped tapetum of the Oxyopidae and Lycosidae (reviewed in Homann 1971; Land 1985a; Fig. 10.5). In spiders with canoe-shaped tapeta, such as the secondary eyes of the Araneidae, the resolution is poor because the image is focused beneath the retina (i.e., underfocused). In contrast, the grate-shaped tapeta of hunting spiders, such as the Lycosidae, reflect focused light to the photoreceptive segments (Land 1985a). While alternative tapetum morphologies have different effects, they all function to increase sensitivity. However, tapeta do have one downside: they can decrease visual acuity as a result of stray light scattering from the tapetum into neighboring photoreceptive units (Morehouse 2020). Some spider families that primarily hunt during the day therefore lack tapeta, including the Philodromidae, Eresidae, and Salticidae (Fig. 10.5). However, we see different suites of adaptations for hunting at night: some species rely on PM eyes with tapeta for prey capture (e.g., Lycosidae; Rovner 1993), while others lack tapeta but have very large PM eyes with large entrance apertures for light gathering (e.g., Deinopidae; Stafstrom and Hebets 2016).

10.3.3.5 Trade-Off Between Resolution and Sensitivity

The diversity in spider eyes provides excellent examples of the well-known trade-off between resolution and sensitivity (reviewed in Warrant and McIntyre 1993; Land 1985a; Land and Nilsson 2012; Cronin et al. 2014; Meece et al. 2021). For an extreme example, the resolution of the principal (AM) eyes of the diurnal Salticidae is ten times better than the PM eyes of the nocturnal Deinopidae, but deinopid receptors are 2000 times more sensitive (Blest and Land 1977); in fact, deinopid PM eyes are so sensitive that they exhibit strong electrophysiological responses to single photons (Laughlin et al. 1980). The eyes of diurnal animals typically have lower sensitivity and thus require an abundance of light to function optimally. This has broad implications for inter- and intraspecific communication, especially in the Salticidae as these spiders encounter colorful prey in their environments (Taylor et al. 2014), and males often display longer wavelength colors to females during courtship (Taylor and McGraw 2013). Under suboptimal circumstances, such as in the shade or at dusk, the spider is at a disadvantage because they cannot reliably discriminate long wavelength colors, such as reds. Under dim light, spiders show attenuated responses to colorful ornaments used in courtship (Taylor and McGraw 2013; Zurek et al. 2015).

Future work, both across and within families, should endeavor to map variation in eye morphology with different lifestyles. For example, in two surveys across at least 34 families, traits that influence resolution and sensitivity, such as relative lens size, rhabdom length, and interrhabdomeric angles, correlate with the foraging mode (L. Sumner-Rooney, personal communication; N. Morehouse, unpublished data).

10.3.3.6 Specializations of Retinal Anatomy

In addition to variation in the optics and photoreceptor structure of eyes, we also see variation in overall retinal structure. As described previously, salticid principal eyes have boomerang-shaped retinas with a central region of increased photoreceptor density, analogous to the foveal region of the vertebrate retina. While the immovable AL eyes of salticids do not achieve the same spatial acuity as the principal eyes, they do have a forward-facing acute zone with a wider field of view (O'Carroll 1989). The Thomisidae and Lycosidae have an anatomical acute zone as well (Blest and O'Carroll 1989), while comparable specialization is lacking in *Cupiennius salei* (Grusch 1994). In *C. salei*, the retinas are shaped like a hemispherical cup (Land and Barth 1992) that is larger and less narrow than that of the Salticidae. The Lycosidae (Melamed and Trujillo-Cenoz 1966) and Thomisidae (Insausti et al. 2012) also have retinas that are hemispherical. However, the retinas of other spiders, such as the Pisauridae, are trough shaped (Williams 1979). The four-layered retinal tiering of the Salticidae discussed previously is certainly not universal; for example, the principal eyes of the wolf spider *Geolycosa godeffroyi* have two layers (Blest and O'Carroll 1989), and those of *C. salei* have only a single layer (Land and Barth 1992). The distribution of photoreceptors and the overall morphology of each layer undoubtedly have functions for vision that are poorly understood, especially for non-salticid spiders, and the number of retinal layers across many spider groups remains poorly described.

10.3.4 Physiological Specializations of Photoreceptors

While the morphological and optical properties of eyes are important for focusing an image, photoreceptors are the cells that actually respond to light. Across virtually all spiders, the retinas of both the principal and secondary eyes have a mosaic of nonpigmented glial cells, pigmented glial cells, and photoreceptor cells. The light-sensitive portions within the photoreceptor cells are cylindrical structures called rhabdoms (Blest 1985). Contained within the rhabdoms are receptive structures called rhabdomeres, which themselves contain highly folded arrays of membrane called microvilli (which have a comb-like shape). Embedded in these membranes are rhodopsins, composed of an opsin protein (Koyanagi et al. 2008) and a vitamin-A-derived, light-sensitive chromophore called retinal (Barth et al. 1993). The rhodopsin maximally absorbs light of a particular wavelength determined by the opsin; absorption causes the retinal to undergo a conformational change that triggers a G-protein-coupled signal transduction cascade. This ultimately depolarizes the cell and transmits an electrochemical signal to the optic nerve (reviewed in Cronin et al. 2014; Hardie and Juusola 2015).

10.3.4.1 Opsin Evolution

Our understanding of the molecular evolution of genes that underlie phototransduction in spiders lags considerably behind other arthropods, but progress is underway. Using transcriptome assemblies from Bond et al. (2014) and Garrison et al. (2016), work by Morehouse et al. (2017) indicates that the canonical components of the rhabdomeric phototransduction pathway identified in insects are also found in the genomes of spiders, although whether these components all serve the same functions remains to be verified. More is known about opsin evolution and expression. The ancestor of spiders and their kin probably had at least four opsin genes, some of which are expressed in the eyes (ocular), brain (extraocular), or both (Eriksson et al. 2013). Four major clades within the opsin gene family have been identified in spiders: Gq-opsin, c-opsin, xenopsin, and tetraopsin (Porter et al. 2012; Ramirez et al. 2016; see Fig. 5 in Morehouse et al. 2017). While the c-opsin, xenopsin, and tetraopsin clades have important implications for elucidating the evolutionary relationships of eye development across arthropods (see Morehouse et al. 2017), of particular interest for phototransduction is the Gq-opsin clade.

Within the Gq-opsin clade, spiders generally have two long-wavelength-sensitive (LWS) opsins and one ultraviolet-sensitive (UVS) opsin (Koyanagi et al. 2008; Nagata et al. 2010, 2012). These are collectively known as rhabdomeric opsins (r-opsins), and these show different expression patterns between the eye types and retinal layers in the salticid *Hasarius adansoni*. In the principal eye retinas, the LWS opsin *Rh1* (which produces a green-sensitive visual pigment when bound to retinal) is expressed in layers I and II, while the UVS opsin *Rh3* is expressed in layers III and IV (Nagata et al. 2012). In the secondary eyes, the *Rh1* opsin is also expressed in the AL and PL eyes, while the LWS *Rh2* (which forms a blue-sensitive visual pigment when bound to retinal) and UVS *Rh4* are expressed in the PM eyes (Nagata et al. 2012). It was long thought that either mygalomorphs had lower opsin diversity than araneomorphs (Fig. 10.5), or there was an undetectable expression in previous studies. To test this, Foley et al. (2020) scored the presence of opsin genes from transcriptomic data in a comprehensive survey of 25 tarantula genera (family Theraphosidae) and found that all subfamilies possessed the full complement of typical arthropod opsins. Across the spider phylogeny, the number and types of r-opsin proteins are similar, but the specific gene copies vary, and these opsins show interesting patterns of losses and duplications (Morehouse et al. 2017). It is possible that opsin expression is linked to visual ecology (e.g., UVS opsins are retained but not expressed in four nocturnal or crepuscular species) and the diversification of colorful signals in the Salticidae (Morehouse et al. 2017), an area ripe for investigation.

10.3.4.2 Temporal Resolution

Temporal resolution, or the ability to resolve successive events in time, exhibits short-term physiological plasticity with changes in the dark- and light-adapted states and varies across nocturnal and diurnal spiders. A key parameter of temporal resolution is the integration time, which is the time it takes a photoreceptor to sample and respond to incoming light (reviewed in Meece et al. 2021). This is often referred to as the “speed” of vision. Longer integration times increase light capture and the signal-to-noise ratio, thereby increasing sensitivity at the cost of reduced temporal resolution (reviewed in Warrant 1999). In the nocturnal spider *C. salei*, dark-adapted integration times of about 138 ms in the PM eyes and 86 ms in the AM eyes were found using intracellular recordings (Pirhofer-Walzl et al. 2007). In the light-adapted state, *C. salei* had an integration time of about 79 ms in the PM eyes and 44 ms in the AM eyes (Pirhofer-Walzl et al. 2007). Evidence suggests that this plasticity might be mediated in part by efferent inputs to photoreceptors in some spiders, such as in the *Argiope* (Yamashita and Tateda 1981, 1983), although it cannot be required because other families, such as the Deinopidae, still show dark adaptation in their PM eyes despite a lack of efferent innervation (Blest 1985). In contrast to nocturnal spiders, spiders active in the day often exhibit shorter integration times, which increases temporal resolution by allowing photoreceptors to respond to successive events more quickly (reviewed in Warrant 1999). Pirhofer-Walzl et al. (2007) approximated the integration time of the AM eye of the diurnal jumping spider *Phidippus johnsoni* to be 42 ms, which is about half that of a dark-adapted AM eye of *C. salei*. A relatively low temporal resolution (and relatively high spatial resolution) seems to be effective for the nocturnal sit-and-wait hunter *C. salei* (Fenk and Schmid 2010, 2011), while diurnal active jumping spiders likely benefit from relatively high spatiotemporal resolution.

Another useful temporal property of an eye is flicker-fusion frequency, or the frequency at which an intermittent light stimulus is perceived as steady. During jumping spider courtship, in which a male and female are involved in rapid reciprocal interactions at close proximity, quicker perceptions of movement might help a male thwart sexual cannibalism. This is also important experimentally because it determines whether video playback during experiments is perceived as fluid motion or a series of static images. Jumping spiders have an estimated light- and dark-adapted flicker-fusion frequency of 90–110 Hz and 50–60 Hz in the AL eyes, respectively (Zurek 2012; D. Zurek, pers. comm.), while *C. salei* has a much lower estimated behavioral flicker-fusion frequency of less than 9 Hz in the PM eyes (Fenk and Schmid 2011). Playback experiments should always aim to use an appropriate frame rate, but currently flicker-fusion frequencies are not well described in other groups.

10.3.4.3 Spectral Sensitivity

Spectral sensitivity, or the wavelength-specific response of photoreceptors, is also variable across families. Color vision requires the comparison of inputs from a minimum of two photoreceptor types with distinct spectral sensitivities (reviewed in Cronin et al. 2014). Spectral sensitivity can be estimated using ERG or receptor potential recordings in response to specific wavelengths of light (e.g., Yamashita and Tateda 1976a; Tapia et al. 2020), through the microspectrophotometry of individual photoreceptors (e.g., Zurek et al. 2015), or by assessing the retinal expression of visual pigments with known absorbance profiles (e.g., Zopf et al. 2013; Sugihara et al. 2016). Investigations of opsin genes suggest that the ancestor of spiders likely had a complement of four visual r-opsins: two LWS opsins (*Rh1* and *Rh2*), one middle-wavelength-sensitive (MWS) opsin, and one UVS opsin (*Rh3*/*Rh*, Morehouse et al. 2017). As discussed previously, photoreceptors of different spectral sensitivities can segregate to particular retinal layers (e.g., jumping spiders) but can be also heterogeneously dispersed across a single layer (e.g., wolf spiders, DeVoe 1972).

Trichromacy, or three color channels, enables an animal to more fully disentangle brightness from wavelength across the visible range of wavelengths (Osorio and Vorobyev 2008) and has independently evolved in the principal eyes of several salticids, facilitated by opsin duplications and subsequent peak spectral sensitivity shifts (Morehouse et al. 2017) or innovations such as spectral filters (e.g., *Habronattus pyrrithrix*, Zurek et al. 2015). This variation provides an excellent opportunity for investigating the mechanisms that underlie spectral sensitivity shifts, the selective pressures that drive the evolution of color vision, and their impact on visual signals. In contrast to principal eyes, secondary eyes generally exhibit monochromacy, or color blindness, which likely helps increase their sensitivity. However, secondary eyes might provide color vision in some species. For example, crab spiders (family Thomisidae), which wait on flowers for prey, appear to have dichromatic secondary eyes based on electrophysiological data (Defrize et al. 2011). UV-, blue-, and green-sensitive photoreceptors are found in the secondary eyes of *Cupiennius salei* (Walla et al. 1996), although extracellular recordings of retinal muscle activity showed a lack of behavioral response when spiders were presented with moving colored stripes over backgrounds of brightness-matched shades of grey, suggesting that they do not distinguish between colors (Orlando and Schmid 2011). Much work remains in characterizing the spectral sensitivities and color vision of spiders at genetic, retinal, behavioral, and evolutionary levels.

10.3.4.4 Polarization Sensitivity

Polarization sensitivity, or the ability to perceive the E-vector orientation of light (i.e., the electric field of an electromagnetic wave, which vibrates orthogonally to the direction of propagation), is useful for complex tasks like navigation and has been described in at least four spider families. At the basis of this ability are photoreceptors with microvilli consistently oriented parallel to each other and perpendicular to incoming light, which therefore respond most strongly to polarized light with an E-vector orientation that is aligned with the microvillar axis (reviewed in Meece et al. 2021). Thus, by comparing the stimulation of nearby photoreceptors with different microvillar orientations, spiders can perceive and respond to light polarization in their environment, such as polarization patterns in the sky and polarized reflections from objects and other organisms. For example, the ground spider *Drassodes cupreu*s (family Gnaphosidae) dedicates a pair of specialized PM eyes to perceive UV skylight polarization (Dacke et al. 1999). Curiously, these eyes have reduced lenses to maximize sensitivity to polarization cues at the expense of resolution (their PM eyes are non-image forming). The PM eyes are so specialized that the tapetum functions as a polarizer when it reflects light, boosting polarization sensitivity further (Mueller and Labhart 2010). The ability to perceive polarized light has also been found in the Lycosidae, which possess a strip-shaped specialized region of aligned rhabdomeres in their principal-eye retinas (Dacke et al. 2001). This specialization is on the ventral retina, which has a receptive field that points to the sky. Similarly, lynx spiders (family Oxyopidae) and *Agelena labyrinthica* (family: Agelenidae) have rhabdomeres of different alignments in the principal-eye retina, some of which are potentially polarization sensitive (Kovoor and Muñoz-Cuevas 1997; Schröer 2017). Interestingly, Schröer (2017) found that the rhabdomeres in other locations of the retina were twisted, which would abolish polarization sensitivity in these nonspecialized regions, potentially improving the signal-to-noise ratio by removing differences in photoreceptor stimulation due to polarization rather than light intensity. In the Salticidae, it has been suggested that a "staircase" pattern of UV-sensitive photoreceptors in Layer IV of the principal-eye retina might support polarization vision (Land 1969a; Eakin and Brandenburger 1971), but *Phidippus* spiders did not appear to use polarization patterns in the sky when pursuing their prey (Hill 1979). Among the species investigated so far that use polarized light cues, polarization vision has been most often supported by the principal eyes, but it is unclear to what extent this applies to other spiders. For a recent review of polarization vision in spiders, see Ortega-Escobar (2017).

10.3.5 Control and Cooperation of Eyes

10.3.5.1 Movable Principal-Eye Retinas

In many families, principal-eye retinas have the ability to move (to our knowledge, eye movement is unstudied in most families). Moveable retinas are particularly useful for spiders, allowing them to alter their gaze direction without alerting potential predators or prey. The masters of eye movements are the jumping spiders. As described in Sect. 10.2.2.2, salticids have six retinal muscles (three pairs, the same number of muscles attached to vertebrate eyes) that direct each eye tube. This suite of muscles enables fine movements, including both translational and rotational movements of the retina in an arc behind the corneal lens. The Ctenidae, Lycosidae, and Thomisidae (Fig. 10.5) have four retinal muscles (two pairs) and are therefore more limited in their repertoire of retinal movements. Like the salticids, these spiders show spontaneous exploratory activity, saccades (up to 15°), tracking to follow objects, and microsaccade twitches (2–4° appearing as rapid quivering) to avoid retinal habituation (i.e., bleaching of photopigments from persistent exposure to the same beam of light that causes the visual image to fade) (reviewed in Morehouse 2020). However, these spiders are unable to use rotational movements to inspect objects further. The principal eyes of *Cupiennius salei* have two muscle pairs, allowing either latero-medial or dorso-ventral movements (Kaps and Schmid 1996), while *Agelena labyrinthica* (family Agelenidae) and many other web-building spiders (Fig. 10.5) have only a single lateromedial pair (Land 1985a; Schröer 2017).

The properties of ocular muscles also determine other movement patterns of the eyes. For example, in *C. salei*, the retinas drift back to the resting position after a saccade because of restoring forces from the opposing stretched muscle (Kaps and Schmid 1996). How tightly synchronized the movements are between eyes also varies. In *C. salei*, a principal-eye retina can be independently directed to a stimulus occurring on its ipsilateral side (Kaps and Schmid 1996), while in salticids, the principal-eye retinas are more tightly coupled, particularly during the active interrogation of a visual stimulus—only during exploratory activity might one retina lead (likely due to lateralization of eye use), after which they “clap” back together to examine an object.

10.3.5.2 Interaction of Eyes

The division of labor between different pairs of eyes has been well studied in only a handful of spider families. The possible interactions between eyes can be usefully divided into two categories: eye pairs that do not share a field of view and eye pairs that do share a field of view.

Eye pairs that do not share a field of view are perhaps more straightforward to understand. For example, as described in Sect. 10.2.2.1, the PL eyes of salticids are oriented toward the rear of the spider. When the PL eyes detect movement, the spider exhibits a rapid turning response and directs its forward-facing AM and AL eyes toward the stimulus. Flattie spiders (family Selenopidae) can very quickly rotate their body using long laterigrade legs and strike prey approaching from any direction with impressive speed and accuracy, possibly using input from their PL eyes to detect prey that is behind them (Zeng and Crews 2018). Thus, in these and other families, the combined field of view of all the secondary eyes gives the spider the ability to monitor a wide area using eyes that individually are quite compact.

Perhaps more interesting are eyes that overlap in field of view, thus providing visual information about the same visual scene from independent visual organs. In many cases, nonmoving secondary eyes may overlap in field of view, either with members of the same pair (e.g., the AL eyes in salticids) or between different sets of secondary eyes. Little is known about how overlapping secondary eye pairs process redundant information. Binocular (or multiocular) overlap might contribute to depth perception, but it is disputed if the eyes of many spiders are spaced far enough apart for this to be a viable strategy. In salticids, Forster (1979) found that jumping spiders with one AL eye masked behaved more or less normally but sometimes slightly misjudged the distance of predatory leaps. The corneal lenses of spider eyes are fixed, and therefore depth perception due to accommodation cannot occur as it does in vertebrate eyes. While retinal tiering and the "stair-case" pattern of photoreceptors in the principal eyes of salticids appear to support depth perception via focus (Blest et al. 1981) or via defocus (Nagata et al. 2012), how this might be accomplished in other spiders is less clear.

For some spiders, we have better insight into how the moveable principal eyes collaborate with the secondary eyes. In jumping spiders and *Cupiennius salei*, the secondary eyes that overlap in field of view (AL and PM eyes, respectively) primarily detect motion and subsequently direct the principal-eye retinas to a target. This collaboration has been verified through electrophysiological recordings of retinal muscles in *Cupiennius* (e.g., Kaps and Schmid 1996; Neuhofer et al. 2009) and eye tracking in salticids (Jakob et al. 2018). It is unclear whether eyes with contiguous and overlapping fields of view can "predict" the trajectory of a moving object, as do the ommatidial facets of a hunting dragonfly compound eye (Wiederman et al. 2017), but recent data suggest that there is an exchange of information between multiple eye pairs in jumping spiders. If a moving object passes through the visual field of the PL eyes to the AL eyes, the principal-eye retinas appear to search for a stimulus with its features (Y. Dolev and X. Nelson, pers. comm.). The presence of moveable principal-eye retinas in other groups (e.g., the active Lycosidae and sit-and-wait Thomisidae) suggests that different eye types share a similar division of labor, but this has yet to be rigorously tested (but see Rovner 1993). The precise targeting of the principal-eye retina seen in jumping spiders may be necessary because the principal-eye retina is so small (see Sect. 10.2.2.2). As described in the previous section, in other spider families, fewer muscles control the principal eyes, and targeting is presumably less precise. However, if the principal eyes have larger retinas and larger fields of view, precise targeting may not be necessary. To understand the evolution of cooperation between moving and stationary eyes, we need phylogenetically informed studies of retinal shape and size, the overlap in field of view between the principal and secondary eyes, the degree of precision in eye movements, the neural pathways between the eyes and the brain (see Sect. 10.3.6), and ecological factors such as hunting strategy. An intriguing hypothesis is that principal-eye retinal movements first evolved to overcome retinal habituation when examining stationary objects. This, along with the unique evolutionary history of each eye type (see Sect. 10.3.2.1), may have set the stage for functional differentiation and the partial release from trade-offs associated with arthropod eye design.

10.3.6 Neurobiology of Vision

After photoreceptors respond to incoming light, electrochemical signals must be processed in the retina or brain for visual perception to occur. Most of what we know about spider brain morphology and function comes from work on jumping spiders and *Cupiennius salei*. In these taxa, the principal and secondary eyes and their neural underpinnings comprise two distinct visual systems (Strausfeld and Barth 1993; Strausfeld et al. 1993). Each eye supplies information to separate brain regions—with some crosstalk between them in salticids—until it is integrated into higher centers (Strausfeld 2012). In salticids, the principal-eye pathways seem to process the features and colors of objects, while the secondary-eye pathways seem to simultaneously process contrast and motion information. Our knowledge about the function of these brain regions is limited by a lack of neurophysiological studies, but hypotheses can be constructed based on their connectivity and our knowledge of relatively similar, yet still quite different, neuroanatomical organization in other arthropods. Here, we provide a brief primer on spider brains and their evolutionary history, after which we describe in more detail how the brain (or synganglion as it is more properly called) is connected to the peripheral visual system.

10.3.6.1 Evolution of Spider Brains

The study of spider brains began with Saint-Remy (1887), who captured unique and diverse structures in elegant drawings. This work was continued by Hanström (1921, 1923, 1935), who applied the Golgi staining technique to spider brains, highlighting their components with great detail. He presumed homology with structures and cell types in insects and crustaceans and thus used similar terminology to describe their visual centers—a (potentially misleading) nomenclatural tradition that persists today. More recent work has largely focused on jumping spiders (e.g., Hill 1975; Duelli 1980; Steinhoff et al. 2017; Long 2021) and *Cupiennius salei* (Babu and Barth 1984; Strausfeld and Barth 1993; Strausfeld et al. 1993), which share similar gross brain anatomy.

The central nervous system of spiders is highly condensed into a mass called the synganglion, which is contained within the cephalothorax, or prosoma. The visual and higher-order centers are found in a region of the synganglion called the protocerebrum, the anterior-most neuromere. The synganglion contains structures called neuropils—composed of synaptic regions and glial processes—which serve as the location of functional integration (Bullock and Horridge 1965; Babu 1965). The cell bodies, or somata, for associated neurons form a rind outside the neuropil. Much like in other arthropods with sophisticated image-forming eyes, the visual system of jumping spiders and *C. salei* consists of successively nested optic neuropils that contain dense networks of stratified interneurons (Strausfeld 2012).

Despite a history of shared terminology, spider brains have a different organization and evolved independently from those of insects and crustaceans (Strausfeld

2012; Lehmann et al. 2015). Many arthropod brains have a midline neuropil called the central body, which is used for complex functions like sensorimotor integration (reviewed in Turner-Evans and Jayaraman 2016). Spiders have an analogous structure called the arcuate body (sometimes also referred to as the central body), which also lies on the protocerebral midline and appears to serve similar functions, although it is part of the principal-eye pathway. Furthermore, spiders lack a dedicated olfactory appendage and its associated processing centers. Many arthropod brains have large areas devoted to olfaction (although some also have very robust optical centers). In insects, olfactory inputs are received by olfactory receptors of the antennae, sent to specific olfactory glomeruli (dense synaptic bundles), then project onto a structure called the mushroom body in the antennal (olfactory) lobe (reviewed in Masse et al. 2009). The mushroom body of insects is also associated with higher-order functions, such as learning (e.g., reviewed in Heisenberg 2003). A structure with similar morphology in spiders, also called the mushroom body, is nested within the secondary-eye pathway but is thought to be primarily used for visual processing (Strausfeld and Barth 1993).

While morphological, developmental, and genetic evidence suggests deep homology of the central and mushroom bodies of insects and their counterparts in spiders (e.g., Homberg 2008; Doeffinger et al. 2010; Wolff and Strausfeld 2015), the debate of homology or convergence has not been fully resolved. Relative to other chelicerates, the mushroom body of spiders (if homologous) has been repurposed for vision (Strausfeld 2012). Such a functional shift from olfactory to visual processing has been documented in the mushroom body of an anosmic water beetle (Lin and Strausfeld 2012). The spider mushroom body does not show immunoreactivity against proteins associated with learning in other arthropods (Wolff and Strausfeld 2015), potentially emphasizing its primary role as a visual center. Neurotransmitter and neuromodulator use in visual centers is best known in the case of *C. salei* (reviewed in Barth 2002), which also appears to be similar to other arthropods (e.g., histaminergic retinula cells).

10.3.6.2 Principal- and Secondary-Eye Pathways

The principal and secondary eyes have separate laminae and medullae, which are the first- and second-order optic neuropils, respectively (Fig. 10.6). The unpaired arcuate body is the third-order optic neuropil of the principal eyes, and the bilaterally symmetric mushroom body is the third-order optic neuropil of the secondary eyes (Strausfeld and Barth 1993; Strausfeld et al. 1993; Fig. 10.6). In jumping spiders and *Cupiennius salei*, all eight eyes innervate distinct laminae and medullae, and each eye of the same type (principal or secondary) shares a similar pathway organization to one another (but see Steinhoff et al. 2020 for a discussion about the PM-eye pathway of salticids). The specific cell types of each pathway are not discussed here in detail as they are described elsewhere (for a review, see Strausfeld 2012; Lehmann et al. 2015).

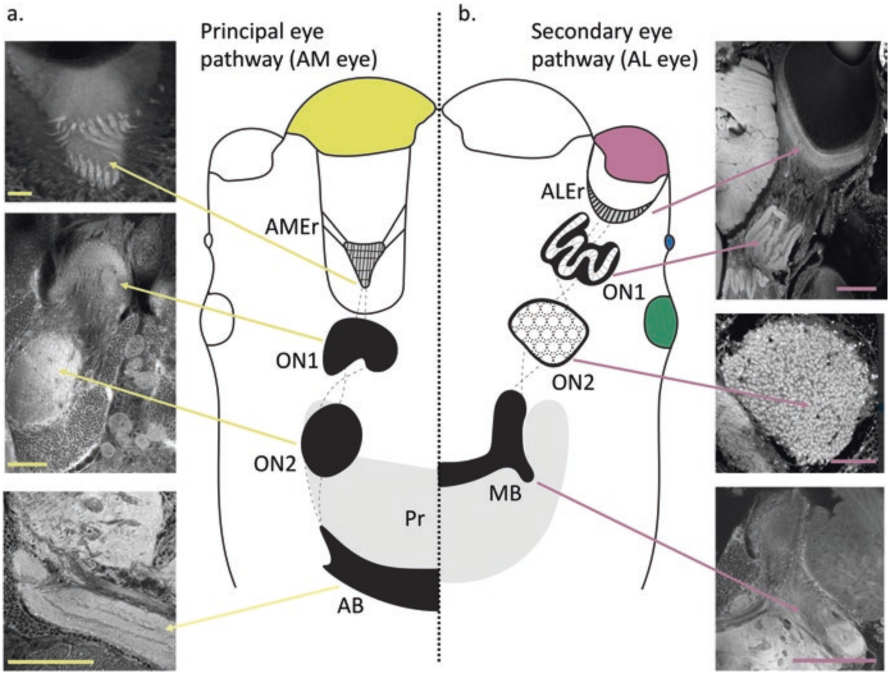

Fig. 10.6 Visual pathways in the brain of *Phidippus audax* depicted in schematic and histological horizontal sections. (**a**) The principal-eye pathway. Shown: AM eye retina (AMEr), lamina (ON1), medulla (ON2), arcuate body (AB), and protocerebrum (Pr). Scale bar represents 50 μm for the AMEr and 200 μm for the rest. (**b**) The secondary-eye pathway. Shown: AL eye retina (ALEr), lamina (ON1), medulla (ON2), and mushroom body (MB). Scale bar represents 50 μm for the ON2 and 200 μm for the rest. The medulla (ON2) of the secondary-eye pathway is comprised of optical glomeruli. Tissue sections were prepared using the methodology described in Long (2018). The diagram is not to scale, and brain structures are not all located in the same plane. The dashed line represents the plane of symmetry. A Nikon Ti confocal microscope (Nikon Instruments Inc., NY) was used for all imaging. Brightness and contrast were adjusted as needed. (Microscope images courtesy of Guilherme Pagoti and the University of Massachusetts Amherst IALS Light Microscopy Core Facility)

In the principal-eye pathway of spiders, projections from the retina enter the rostral edge of the lamina, where they are met by local interneurons (Strausfeld et al. 1993). In salticids, retinula axons are bundled (Oberdorfer 1977) but not pooled (Land 1969a), including those from different retinal layers. The lamina is layered, consisting of four distinct terminal zones in the salticid *Hasarius adansoni* (Nagata et al. 2019). These terminal zones (TZs) correspond to the termination sites of photoreceptor axons from specific retinal layers. For example, green-sensitive photoreceptors from layers I and II terminate in TZ1 and TZ2, respectively. In contrast, lateral UV-sensitive photoreceptors from retinal layers III and IV terminate in TZ3, whereas UV-sensitive central photoreceptors from these layers terminate in TZ4. In all instances, retinotopy is preserved in the TZs, suggesting that spatial information is preserved at this stage. However, lateral processes from UV photoreceptors terminating in TZ3 also innervate TZ1, suggesting that TZ1 may also be able to extract spectral information. Further, interneurons running between TZ1 and TZ2 may allow for the comparison of defocus information postulated to provide depth cues. Thus, TZ1 and TZ2 may be the initial source of spatial, spectral, and depth information incoming from the principal eyes (Nagata et al. 2019). While it is unclear if this organization is common across salticids, at least two adjoining terminal subunits have been noted by other investigators using different species (Hill 1975; Oberdorfer 1977; Steinhoff et al. 2020). In other arthropods, such as insects, lamina cells are thought to filter signals spatially and temporally (e.g., Stöckl et al. 2020). In spiders, projections exit the lamina and target different layers of the medulla (Strausfeld et al. 1993; Hill 2022). In jumping spiders, the medulla likely plays a major role in processing the shape and other features of an object, benefitting from the refined signals acquired from the lamina. It is important to note that in the principal-eye pathway of spiders, no projections that bypass the lamina have been found, such as those in the chromatic channels of flies that target deep layers of the medulla (e.g., Yamaguchi et al. 2008). From the medulla, projections extend to the ipsilateral flange of the arcuate body (Strausfeld et al. 1993). The arcuate body is layered by stratified amacrine and intrinsic neurons, with columnar output neurons that project to areas of the mid-brain (Strausfeld et al. 1993).

In the secondary-eye pathway of salticids and other highly visual hunters, discrete groups of lamina neurons terminate in individual optical glomeruli of the medulla. The axons from the lamina nearly twist 180° before projecting to glomeruli, forming partial chiasmic "chunks" (Strausfeld and Barth 1993; Strausfeld 2012). Perhaps similarly, strepsipteran insects have an organization that subdivides the visual field for "chunk sampling" (Buschbeck et al. 2003). Chiasmic chunking might lend itself to processing adjacent units of visual space at the expense of reduced panoramic image integration. The glomerular organization of the medulla also has analogs in other arthropod brains. Glomerular organization is thought to be efficient given its broad evolutionary convergence for olfaction across phyla (Hildebrand and Shepherd 1997; Eisthen 2002), and some researchers suggest that olfactory and optic glomeruli in arthropods share an organizational ground pattern (Strausfeld et al. 2007; Mu et al. 2012). The optical glomeruli in the lateral protocerebrum of *Drosophila melanogaster* receive nonretinotopic inputs from the lobula yet convey the presence and location of specific visual features to motor centers (Wu et al. 2016). In visually hunting spiders, glomerular chunking may reduce the integration of directional motion across the visual field but enhance the perception of motion in small units. This might help direct principal-eye retinas to a visual target (Strausfeld 2012), facilitated by whole-body turns (fixations) or eye-tube movements (saccades). This organization might function similarly to the small-target motion-detector neurons of predatory insects, such as dragonflies and robber flies, which help them ignore background panoramic motion to pursue a moving target (Buschbeck and Strausfeld 1996; Barnett et al. 2007). In salticids, a mysterious second-order neuropil associated with the secondary eyes (called the "lateral eye neuropil" by Hill 1975, "L2" by Steinhoff et al. 2020, and the "secondary eye lateral neuropil" by Long 2021, the last of which is used hereafter) lacks glomerular organization and bypasses the medulla, which might preserve wide-field panoramic information. However, other investigators have suggested that glomerular organization preserves retinotopy (evidenced by a lack of observable lateral connections), while retinotopy is lost in the secondary eye lateral neuropil, which might enable faster processing of movement (Steinhoff et al. 2020). In the visually guided hunting spiders described in Long (2021), glomeruli then project onto distinct contiguous regions of the ipsilateral mushroom body, which is composed of parallel layers of intrinsic fibers originating from small globuli cells (Strausfeld and Barth 1993; Long 2021). The mushroom bodies are connected by large nerve fibers (the mushroom body "bridge") that cross the midline of the protocerebrum, rostral to the protocerebral commissure. Large output neurons (perhaps similar to those found in the lobula plate of insects) from the mushroom body to the motor centers suggest a role for the mushroom body in behaviors such as prey pursuit (Strausfeld and Barth 1993).

In salticids, the AL eye laminae send direct projections to the arcuate body (Steinhoff et al. 2020), and the principal eye laminae send direct projections to the mushroom body (Strausfeld 2012), affording the opportunity for crosstalk between the two pathways. Centrifugal projections, which originate from higher-order neuropils and target neuropils of a lower order (i.e., so that information can flow in both directions), occur between the medulla and lamina and might allow for the refinement of signals (e.g., accounting for rapid changes in luminance). Secondary-eye optical nerve tracts appear to terminate on the ventral surface of the arcuate body, the probable distal-most location of convergence between the two pathways, although these connections are not well mapped (Weltzien 1988; Long 2021). Extracellular recordings show that, in salticids, a protocerebral region just behind and below the arcuate body responds to inputs from both the secondary and principal eyes (Menda et al. 2014).

10.3.6.3 Variation in Neuromorphology

While brain Bauplans tend to be conserved among closely related taxa, even over geological time (Strausfeld 2019), neural tissue is energetically expensive in both its development and maintenance (Hasenstaub et al. 2010). This means that strong selective pressures can drive divergent brain evolution; specifically, we expect brains to be reduced when they are too costly to maintain and enlarged (or more complex) if fitness benefits outweigh the energetic costs. For example, amphipods of the suborder Hyperiidea have highly variable optic lobe organization and size, correlated with ecological factors, such as the ambient light environment (Lin et al. 2021). Perhaps for similar reasons, visual pathway organization and the percentage of brain volume devoted to visual processing in spiders vary across families (Long 2021).

The principal-eye pathway organization appears to be highly conserved across families (Strausfeld et al. 1993; Kovoor et al. 2005; Nagata et al. 2019; Steinhoff et al. 2020; Long 2021), although there is conspicuous variation in neuropil volume and shape. The arcuate body is relatively robust in most of the species investigated so far (e.g., Weltzien and Barth 1991; Long 2021), likely because of the pivotal role it plays in other functions that would presumably constrain its evolution. However, the arcuate body appears to be somewhat more elaborate in visual hunters (Strausfeld 2012; Long 2021). The volume and shape of the first- and second-order neuropils are highly variable. The volume (or perhaps, more importantly, density) of these regions might be influenced by the extent to which particular information, such as form or color, is important to the spider. Variation in shape might also be influenced by the position and architecture of the retina or eye.

Tremendous variation exists in the secondary-eye pathways across families, as originally noted by Hanström (1935). There are key differences among salticids (Steinhoff et al. 2020), *Cupiennius salei* (Strausfeld and Barth 1993), the less studied orb weavers (Park et al. 2013; Park and Moon 2013), and other spiders. In a recent landmark comparative study, Long (2021) found that the Antrodiaetidae, Hypochilidae, Filistatidae, Scytodidae, and Pholcidae (Fig. 10.5) had the simplest secondary-eye pathways, with underdeveloped laminae, absent or highly reduced medullae, and no apparent mushroom bodies. The Antrodiaetidae was the only mygalomorph represented in this study, and the latter four are relatively basal araneomorphs (Fig. 10.5), all of which are not highly visual (see Sect. 10.3.1). The Araneidae and Deinopidae (Fig. 10.5) had large laminae, absent or highly reduced medullae, and large mushroom bodies. The enlarged mushroom bodies of the Deinopidae were unsurprising, considering their heavy reliance on prey movement cues when hunting at night, but the robust laminae and mushroom bodies of the relatively sedentary orb weavers were an unexpected finding (S. Long, pers. comm.). The Theridiidae, Nephilidae, Amaurobiidae, Agelenidae, and Eutichuridae (formally known as Cheiracanthiidae) (Fig. 10.5) had laminae and some evidence of reduced medullae and mushroom bodies. The Cheiracanthiidae had a simpler secondary-eye pathway than its phylogenetic position would suggest, suggesting a secondary reduction in complexity (Fig. 10.5). Finally, the Ctenidae, Oxyopidae, Pisauridae, Lycosidae, Thomisidae, Philodromidae, and Salticidae (Fig. 10.5) were the most complex, with large laminae, medullae formed from optical glomeruli, and prominent mushroom bodies. We suggest that readers consult Long (2021) for a more detailed discussion of the differences found among groups.

The number of optical glomeruli, when present, varied across families, with the highest density belonging to the Salticidae. The number and connectivity of glomeruli likely relate to the number of visual parameters that can be processed (Strausfeld 2012). Each glomerulus is estimated to have at least a few hundred synapses (about 400 in the salticid *Evarcha arcuata*, Duelli 1980). It is unknown how many retinula cells are represented within each glomerulus and if the ratio is plastic (Long 2021). The degree of chunking (i.e., the number of receptors represented in each glomerulus) would impact their receptive fields and possibly the precision of small-field motion detection and retinal targeting. The presumed ancestral ground pattern of the secondary-eye pathway contains laminae and medullae as first- and second-order neuropils, respectively, so losses are likely to arise from extensive reduction or merging events (Long 2021). Further phylogenetically informed studies should correlate neuromorphology (e.g., Long 2021) and the volume of higher-order centers (e.g., Steinhoff et al. 2018) with different lifestyles and ecological conditions, such as sociality, the complexity of visually guided behaviors, or ambient light environment.

It is presently difficult to draw conclusions about the ecological pressures that drive variation in pathway organization and neuropil shape or volume and the extent to which this variation is related to the diversification of spiders. The homology or convergence of neuromorphological characters remains mysterious without more extensive taxon sampling and ancestral state reconstructions. Chelicerate visual system evolution remains enigmatic, but some investigators have been meticulously conducting new neuroanatomical studies (e.g., Lehmann and Melzer 2021; Brenneis 2022). Recently, methods for sectioning using classical histology, confocal microscopy (Long 2018, 2021), and X-ray microcomputed tomography (Sombke et al. 2015; Steinhoff et al. 2017; Stafstrom et al. 2017) have been refined for use in spiders. Even within investigated families, transmission electron microscopy studies (e.g., Lehmann and Melzer 2018b) are needed to ascertain if unidentifiable neuropils have been lost or fused. Neuronal tracing studies are needed to map the connectivity of the principal- and secondary-eye pathways. Of particular interest is the presence and connectivity of a mushroom body in basal spider groups (i.e., Liphistiidae) as it is still unclear if the mushroom body of spiders is homologous with other arthropods or convergently evolved. If homologous, it is possible that the extensive reduction of the mushroom body in basal groups coincides with the loss of an olfactory appendage when spiders diverged or the mushroom body may have not yet merged into the secondary-eye pathway. The presence of a mushroom-body-like structure, apart from the secondary-eye pathway, has been found in basal mygalomorphs (e.g., Antrodiaetidae in Long 2021; the old-world tarantula *Poecilotheria* in Babu 1965). It would also be of interest to investigate the mushroom bodies of other chelicerates, which are likely olfactory (e.g., amblypygids; Sinakevitch et al. 2021). Electrophysiological studies (e.g., Menda et al. 2014) are required to determine the role of each neuropil (Barth 2002). This work has been neglected due to logistical difficulties associated with pressurized spider prosomas (hydrostatic pressure from hemolymph is used to extend the legs). Spiders rapidly perish if an incision is made in their cuticle, and their brain wobbles with each heartbeat. Fortunately, single- and multiunit extracellular recordings of higher-order centers using thin tungsten microelectrodes have been finally deployed in the jumping spider *Phidippus audax* (Menda et al. 2014; Shamble et al. 2016; A. Winsor, unpubl. data) and the net-casting spider *Deinopis spinosa* (Stafstrom et al. 2020). Across spiders, it is possible that corresponding neuropils are processing different types of information, especially when considering divergent pathway organizations.

10.4 Conclusions and Future Directions

In this section, we wish to highlight a few areas that we think are especially interesting for future work. First, as we have seen, spider visual systems show enormous variation, which is ripe for comparative study. Given that comprehensive, robust, and largely congruent backbone phylogenies are available for spiders (e.g., Bond et al. 2014; Garrison et al. 2016; Wheeler et al. 2017), inferences at the family level or below should be feasible (e.g., Wolff et al. 2022). We currently have a great deal of data on variations in eye arrangement, eye morphology, photoreceptor properties, and neuromorphology for many spider taxa. By strategically adding to this data set and combining it with environmental and behavioral traits, we have many opportunities to understand the selection pressures that led to visual system specialization.

A second, related point is that the distributed visual systems of spiders allow us to investigate how natural selection can act independently on each pair of eyes to overcome functional trade-offs and to understand how the eyes work together. By distributing vision across multiple eyes with different specializations, spiders face relaxed body-size constraints on visual function, which are typically encountered by small animals that mostly rely on a single type of eye (e.g., Rutowski et al. 2009; Warrant and McIntyre 1993). Eye-masking experiments offer the opportunity to study the properties of different visual pathways in isolation and to see how information from multiple eyes is integrated. As elaborated in Sect. 10.3.5.2, our most in-depth knowledge about how eyes divide up tasks is based on only a few families. We especially encourage the study of vision in species that do not appear to rely much on visually based behavior but still have surprisingly robust visual pathways in their central nervous system (e.g., Araneidae) (Long 2021).

Third, the degree to which spider visual processes are flexible is an interesting area. How bottom-up and top-down mechanisms regulate visual cognition is ripe for exploration in invertebrates, especially spiders (reviewed in Winsor et al. 2021). For example, state-dependent modulation of vision, which occurs when changes in physiological states, behavioral states, or environmental conditions impact visual processing (Cheng and Frye 2020), has been virtually unexplored in spiders. How inputs from other sensory modalities influence visual attention is poorly understood outside of salticids and lycosids.

Fourth, how visual information is processed in the spider's brain has just begun to be explored. Researchers have shown that areas in the arcuate body region of the jumping spider brain respond to particular visual images (Menda et al. 2014) and sounds (Shamble et al. 2016). Next, in salticids, recording from more peripheral areas of the separate pathways between the brain and the principal and secondary eyes will help demonstrate exactly where different types of visual information are processed and then integrated. In addition, expanding this work beyond salticids will, of course, be extremely informative, especially given the vast variation in neural architecture across families (Long 2021).

Finally, using spiders for bioinspired engineering solutions is another area of potential research. For example, the computationally efficient construction of a system like that of jumping spiders, which is broadly tuned to lower-resolution, motion-sensitive inputs yet can strategically direct a higher-acuity apparatus to certain stimuli, has already inspired robotic camera systems (Tonet et al. 2008). Similarly, Guo et al. (2019) designed a compact depth sensor inspired by jumping spiders' image-defocusing mechanism.

The visual systems of spiders are both extremely variable and impressively capable. Our knowledge of spider vision is being pushed forward by the collaborative efforts of interdisciplinary researchers worldwide. Much exciting work remains as we attempt to understand how spiders see the world.

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