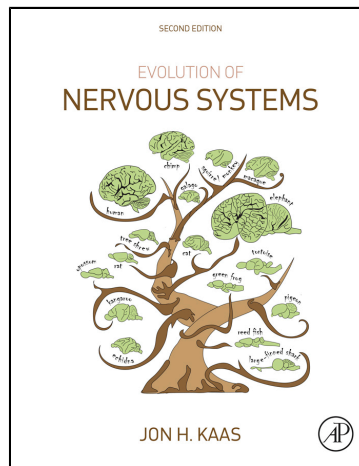


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## 1.19 Structure and Function of Regional Specializations in the Vertebrate Retina

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<b>1.19.1</b>	<b>Introduction</b>	351
<b>1.19.2</b>	<b>Retinal Specializations: Morphology and Functional Hypotheses</b>	352
1.19.2.1	Retinal Area	352
1.19.2.2	Radial Anisotropy	357
1.19.2.3	Visual Streak	357
1.19.2.4	Fovea	359
1.19.2.5	Area Gigantocellularis	364
<b>1.19.3</b>	<b>Future Directions</b>	365
1.19.3.1	Behavioral Approaches	365
1.19.3.2	Cell Type-Based Approaches	366
1.19.3.3	Optical Approaches	367
1.19.3.4	Developmental and Genetic Approaches	367
<b>1.19.4</b>	<b>Conclusion</b>	368
<b>References</b>		368

### Abstract

Visual sensory demands vary substantially across vertebrates. Different visual sensory components have evolved to meet these sensory demands and enhance visual behavioral performance. One of these components is the retinal specialization, which is a portion of the retina with generally high ganglion cell densities, which increase spatial resolving power. Retinal specializations are relevant from a functional perspective because animals can align these “acute zones” with objects of interest within a localized region of their visual space, consequently affecting different behavioral dimensions. In this chapter, we reviewed the different types of retinal specializations found in vertebrates (retinal *area*, fovea, visual streak, radial anisotropy, area gigantocellularis) by discussing the different hypotheses proposed over decades to explain their function. Empirical tests on the functional properties of these different retinal specializations have been limited, which constrains our ability to understand the functional evolution of the vertebrate eye. We derive specific predictions from each of the hypotheses put forward to identify their degree of overlap. Finally, we provide some future directions as to how to test these functional hypotheses by integrating physiological and behavioral approaches. Testing these functional hypotheses will enhance our understanding of the relationship between the eye and the physical environment, and ultimately the visual ecology of vertebrates.

### 1.19.1 Introduction

The retina is a complex, multilayered neural tissue at the back of the eye and upon which an image of the visual surroundings is formed. From a functional perspective, the retina receives visual information that is essential for an organism to interact with its environment successfully (Collin, 1999). From an evolutionary perspective, the retina has adapted to the visual needs of different species, giving rise to a wide diversity of retinal configurations across vertebrates (Walls, 1942; Hughes, 1977). This diversity is reflected in the different types, numbers, and positions of retinal specializations, which are regions in the retina that provide high visual resolution or that outperform the rest of the retina in various functions (eg, improved detection of movement).

In the retina, photoreceptors (ie, rods and cones) transform light energy into electrical signals so that a neural image can be formed in the brain (Collin, 1999). Through synaptic connections to horizontal and bipolar cells, this visual information is

transferred to the retinal ganglion cells, whose axons come together to form the optic nerve and carry the electrical signals to the visual brain centers (McIlwain, 1996). Ultimately, therefore, the density of retinal ganglion cells limits how much of the information captured by the photoreceptors reaches the brain (Collin, 1999).

The density of retinal ganglion cells across the retina is heterogenous, with some regions having higher cell densities than others. Areas of high retinal ganglion cell density increase the visual resolution of the visual field they subtend (Meyer, 1977). Certain retinal specializations are characterized by high ganglion cell densities, thus increasing image sampling and visual acuity. Because such retinal specializations occupy a relatively small proportion of the retina, they also subtend a small area of the visual field. This has important functional implications, as animals can align these “acute zones” with objects of interest within a localized region of their visual space. For example, Eastern meadowlarks (*Sturnella magna*) direct their retinal acute zone to the area just above the horizon, where predators are most likely to appear (Tyrrell et al., 2013). Similarly, archerfish (*Toxotes chatareus*) align their retinal acute zones at prey situated above the water before projecting a water dart (Temple et al., 2010).

The different types of retinal specializations considered here include retinal *area*, fovea, visual streak, radial anisotropy, and area gigantocellularis. Despite several reviews describing the diversity of retinal specializations (eg, morphology, number, position in the retina) across vertebrate species (Walls, 1942; Collin, 1999; Collin and Shand, 2003), no study has systematically reviewed the hypotheses proposed and empirical tests conducted to explain the function(s) of these specializations. Thus, our goal here is twofold. First, we compiled the functional hypotheses of the different types of retinal specializations from the literature and discuss the empirical tests performed on different vertebrate species. Second, we provide some future directions about how to test these functional hypotheses by integrating physiological and behavioral approaches.

Establishing the functional properties of different retinal specializations is necessary to understand the evolution of the vertebrate visual system (Pushchin and Karetin, 2009), thereby enabling us to answer such questions as “How do retinal specializations help optimize the sampling of visual information?” and “How have retinal specializations coevolved with behavior?” Currently, very little empirical evidence exists on the function of retinal specializations across vertebrates, although many hypotheses have been proposed. Here, we review the different types of retinal specializations by briefly characterizing their morphology, present the different hypotheses to account for their function, and then discuss the empirical evidence supporting some of these hypotheses (see Table 1, Hypotheses 1–19).

## 1.19.2 Retinal Specializations: Morphology and Functional Hypotheses

### 1.19.2.1 Retinal Area

Chievitz (1889, 1891) was the first to describe a “retinal *area*” (or simply *area*) when referring to the macula lutea of humans. Macroscopically, the *area* in vertebrates is a thickening in the retina due to a marked increase in the density of retinal neurons (eg, photoreceptors, interneurons, ganglion cells) (Figs. 1B and 2; Kahmann, 1935). Because increased neuron density mediates high-acuity vision, positioning an *area* within the portion of the visual space of most interest to the organism is critical in the detection of predators, prey, and conspecifics (Collin, 1999, 2008; Tyrrell and Fernández-Juricic, 2015). Thus, *areae* for high-acuity vision have been found in many different locations throughout the retina (central, dorsal, ventral, temporal, nasal), and in some species more than one such *area* exists (Table 2). Directional terms have been used to describe the position of the *area* in the eye, such as *area temporalis*, *area nasalis*, and *area centralis*. However, many studies use the term *area centralis* to denote the *area* even when its location may not be central (Ito and Murakami, 1984; Collin, 1999; Mass and Supin, 2003).

Five hypotheses have been proposed for the function of retinal *areae* (Table 1, Hypotheses 1–5). First, the *area* was hypothesized to provide high visual resolution in the sector of the visual field it subtends (Slonaker, 1897; Collin, 1999), due to the high density of retinal neurons (photoreceptors, interneurons, and retinal ganglion cells) (Table 1, Hypothesis 1). As discussed by Hughes (1977), specific cell types have heterogeneous distributions across the retina, meaning some types may be more prevalent than others within an *area*. Empirically, retinal ganglion cells within the *area* of the cat, *Felis catus*, have been shown, through both physiological and morphological approaches, to consist largely of medium (X-type) cells (Fukuda and Stone, 1974; Rowe and Stone, 1976; Tancred, 1981). These “brisk-sustained” cells have been classified quantitatively by the small size of their receptive field (Cleland et al., 1973) and have been shown to subserve resolution functions (Cleland et al., 1971) due to their projection primarily to the lateral geniculate nucleus (LGN; a major brain center involved in pattern vision) (Cleland and Levick, 1974; Fukuda and Stone, 1974; Hughes, 1977). Retrograde transport studies have confirmed that X-type ganglion cells project predominately to the LGN, with very few projections to the superior colliculus (Kelly and Gilbert, 1975; Hughes, 1977).

Rahman et al. (2006) hypothesized that the function of the *area* may actually differ between species depending on the densities of particular types of retinal ganglion cells within a specific *area* (Table 1, Hypothesis 2). This is an important concept because of the large variety of retinal ganglion cell types with different functional properties (at least 17 distinct types have been classified as parasol, midget, small bistratified, etc.; Field and Chichilnisky, 2007). For example, midget retinal ganglion cells are reported to be the primary carriers of color vision signals, whereas small bistratified retinal ganglion cells carry a specific color signal (Field and Chichilnisky, 2007). Some types of retinal ganglion cells containing melanopsin (ipRGCs) are intrinsically photosensitive, rendering their light responses independent of photoreceptor input (Berson, 2002). Even within ipRGCs, there are several subtypes serving diverse functions (Schmidt et al., 2011). Therefore, high-density retinal regions may contain ganglion cell types with different functions. As mentioned earlier, the *area* of the cat is predominantly composed of X-cells, but also contains the functionally different W-cells (Fukuda and Stone, 1974; Rowe and Stone, 1976; Tancred, 1981). These X-cells mediate

**Table 1** The functional hypotheses, empirical testing, our predictions for the hypotheses of all retinal specializations, and suggestions as to how these hypotheses could be tested based on our predictions

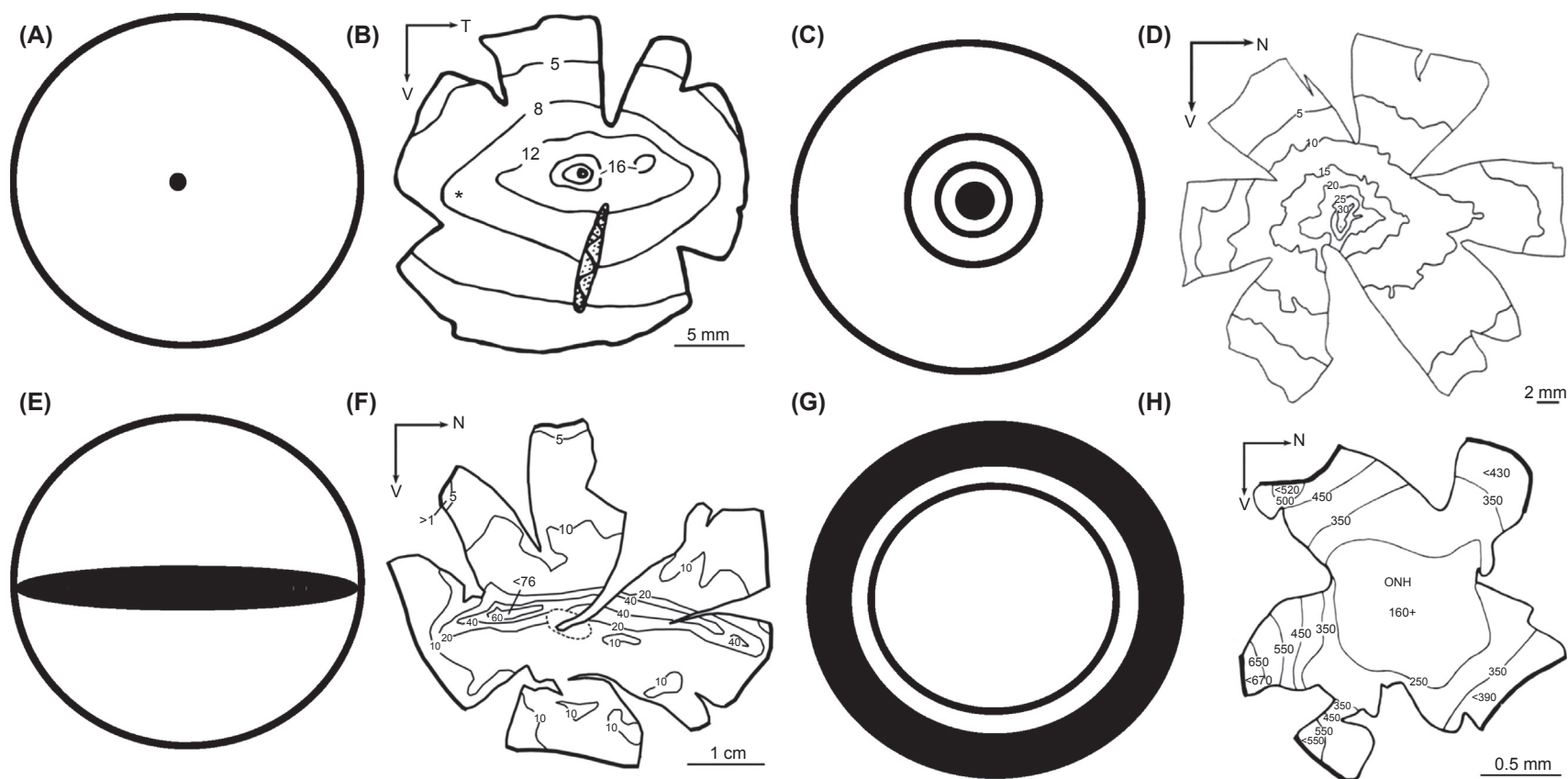
Type of specialization	Functional hypothesis	Empirically tested?	Predictions	How to test
Area	Area of highest cell density provides high visual resolution	Cleland et al. (1971), Cleland and Levick (1974), and Fukuda and Stone (1974)	The <i>area</i> will be aligned on objects of interest	Behavior
Area	Different functions dependent on the functional properties of different types of retinal ganglion cells within a specific <i>area</i>	Fukuda and Stone (1974) and Rowe and Stone (1976)	Animals will use <i>areae</i> in different visual tasks, such as for detecting moving prey and predators, static close prey, distant static prey/predators, etc.	Cell distribution/type
Area	Multiple functions depending on neural projections to multiple brain regions.	Cleland and Levick (1974), Fukuda and Stone (1974), and Rowe and Stone (1976)	Animals will use <i>areae</i> in different visual tasks, such as for detecting moving prey and predators, static close prey, distant static prey/predators, etc.	Cell distribution/type
Area	Fixation within the binocular field	Stone 1966, 1983; Stone et al. (1973)	Animals fixate their <i>areae</i> with the object in the binocular field	Behavior
Area	High-resolution viewing of static near objects	Bloch and Martinoya (1982)	The <i>area</i> will be aligned on static objects close to the animal, and the fovea will be used for objects far from the animal	Behavior
Radial anisotropy	High-acuity peripheral vision	No	Animals would use it to visualize objects entering the visual field with high acuity	Cell distribution/type
Radial anisotropy	Movement detection	No	Animals would use it to detect movement of objects entering the visual field	Behavior, cell distribution/type
Visual streak	High visual acuity	No	Animals will align streak to environmental axis of greatest importance (eg, vertical in trees, horizontal in open areas)	Behavior
Visual streak	Multiple functions based on type of cells in visual streak	Fukuda and Stone (1974) and Rowe and Stone (1976)		Cell distribution/type
Visual streak	Increased visual resolution and improved detection of weak visual cues	No		Cell distribution/type
Fovea (deep)	Highest acuity of all retinal specializations	Walls (1942), Gaffney and Hodos (1973), and Fox et al. (1976)	Position the fovea on object of most interest within the visual space	Behavior

(Continued)

**Table 1** The functional hypotheses, empirical testing, our predictions for the hypotheses of all retinal specializations, and suggestions as to how these hypotheses could be tested based on our predictions—cont'd

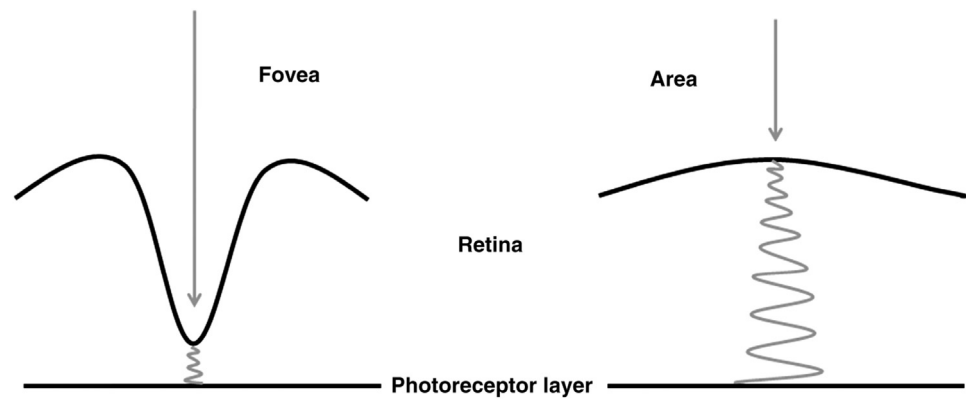
Type of specialization	Functional hypothesis	Empirically tested?	Predictions	How to test
Fovea	Reduction in chromatic aberration	No		Optical
Fovea	Image magnification due to vitreoretinal refractive indices and increased focal length	Valentin (1879), Walls (1937), and Snyder and Miller (1978)	Animals will place fovea on object of interest for a magnified, high-acuity visual sample	Optical
Fovea	Reduce light scattering by clearing of retinal tissue and/or vasculature	Weale (1966)	Image should be less distorted/more clear = higher resolution	Optical
Fovea (deep and shallow)	Image distortion for movement detection and image fixation	Pumphrey (1948), Bloch and Martinoya (1982), and Maldonado et al. (1988)	Animals will use the deep fovea while scanning the environment to detect moving objects. They can then fixate on that object due to the distortion of the image, allowing tracking	Behavior, optical
Fovea	Sensitive, directional focus indicator	Harkness and Bennet-Clark (1978)	Animal will use the fovea as a focus cue for accommodation	Optical
Fovea	Skewing of image from foveal periphery to center for perception of depth	Steenstrup and Munk (1980)	Animals will project fovea onto cryptic object to distinguish camouflaged animals from the visually similar background	Behavior, optical
Area gigantocellularis	Movement detection	Boycott and Wässle (1974), Cleland et al. (1975), Peichl and Wässle (1981), Bailes et al. (2005), Hayes et al. (1991), and Coimbra et al. (2006) (only with limited taxa)	Animals will use an area gigantocellularis while scanning the environment to detect moving objects	Behavior, cell distribution/type
Area gigantocellularis	Sensitivity enhancement at low light levels	No	Deep-sea animals use the area gigantocellularis during foraging bouts in low light levels to enhance sensitivity	Behavior, cell distribution/type

Although empirical testing has been performed for most of the functional hypotheses, they are limited and are generally unresponsive to one another. Empirical testing is also very limited across taxa.



**Figure 1** Schematic representations of different retinal specializations. (A) Schematic representation of a fovea and (b) topographic map of a foveate retina (black vulture *Coragyps atratus*, Inzunza et al., 1991), (C) schematic representation of an area or area gigantocellularis and (D) topographic map of a retina with an area centralis (Indian blue-shouldered peafowl *Pavo cristatus*, Hart, 2002), (E) schematic representation of a visual streak and (F) topographic map of a retina with a visual streak (Western gray kangaroo *Macropus fuliginosus*, Beazley, 1985), and (G) schematic representation of a retina with radial anisotropy and (H) topographic map of a retina with radial anisotropy (burrowing frog *Heleioporus eyrei*, Dunlop and Beazley, 1981).





**Figure 2** Cross-sectional example showing the difference between a fovea and an *area*. A fovea is a pitted invagination of the retinal tissue, whereas an *area* is characterized by an increase in retinal thickness due to an increase in retinal neuron number. Also shown is how the fovea may reduce light scattering due to a reduction of retinal tissue or retinal vasculature within the path of incident light, which would otherwise impede its direct transmission to the photoreceptor layer (Walls, 1937; Weale, 1966) (Table 1, Hypothesis 15).

**Table 2** Examples of the wide variety of placements and numbers of *areae* within the retina in different species

Placement of area	Animal example	Number of areae	References
Central	Peafowl, mallard	1	Hart (2002) and Rahman et al. (2007)
Dorsal	Eastern shovelnose ray	3	Litherland and Collin (2008)
Dorsotemporal	Brown-eared bulbul	2	Rahman et al. (2008)
Temporal	Beluga whale	2	Mass (2001)
Ventrotemporal	Ghost bat	1	Pettigrew et al. (1988)
Ventral	Bigfin pearleye	1	Collin and Partridge (1996)
Ventronasal	Hatchetfish	1	Collin and Partridge (1996)
Nasal	Coral cod	1	Collin and Partridge (1996)
Dorsonasal	Staghorn damselfish	3	Collin and Pettigrew (1988a)

high-resolution vision, whereas W-cells probably serve to detect weak/dim visual stimuli (see later discussion; Rowe and Stone, 1976). If the densities of different functional subtypes of retinal ganglion cells within the *area* do indeed differ between species, then multiple types of *area* could be defined based on the relative densities of these different cell types (Rahman et al., 2006).

The target in the brain to which retinal ganglion cells within an *area* (or any retinal specialization) project should also be highly indicative of the *area's* function. Based on this idea, Blakemore (1969) hypothesized that an *area* may have multiple functions (eg, high visual resolution, stereopsis, etc.) depending on the degree to which the central projections of the axons of retinal ganglion cells within the *area* are crossed (ipsilateral vs contralateral) and, thus, the different degrees of binocular representation in the brain (Table 1, Hypothesis 3). In the cat, for example, ganglion cells within the nasal and temporal halves of the retina have been shown to project to different sides and different areas of the brain (eg, LGN and superior colliculus), separated by what is termed the naso-temporal division, or the transition between the limits of the *area* and the remaining retina (Stone, 1966; Stone and Fukuda, 1974; Terao et al., 1982). Since the *area* is often located at the edge of the nasotemporal division, the ganglion cells may be projecting to different regions in the brain and thus may be involved in different functions (Wylie and Iwaniuk, 2012). A good example is the three-toed sloth (*Bradypus variegatus*), whose *area* is split by the decussation of ipsilateral and contralateral projections and, as suggested by Costa et al. (1987), could be involved in both high visual resolution and binocular vision (depth perception). Binocular representation of an image must be present in at least one hemisphere for stereopsis to take place (Blakemore, 1969; Stone, 1983). Bilateral representation of the *area* would accomplish this through binocular vision (Blakemore, 1969; Stone, 1983). However, this may not apply to all vertebrates, as some (eg, birds and many fishes) have complete decussation of retinal neurons and thus no bilateral representation (Gelatt et al., 2013). In contrast to birds and mammals, retinal neuron proliferation is continuous throughout life in some fishes, amphibians, and reptiles allowing the topography of retinal ganglion cells to change with age (Stone, 1983; Shand et al., 2000). For example, the position of the *area* in the black bream *Acanthopagrus butcheri* and the mackerel icefish *Champscephalus gunnari* "migrates" across the retina as they grow in response to a switch from a pelagic to a benthic foraging habitat (Shand et al., 2000; Miyazaki et al., 2011). Consequently, Blakemore's (1969) hypothesis may only apply to some taxa and not others.

Through analyses of the projection patterns of different retinal ganglion cell types (eg, X-, Y-, W-cells), Stone (1966, 1983; Stone et al., 1973) showed that the mammalian *area* is consistently located at the junction of the axis of the nasotemporal division and the visual streak and consistently projects to brain regions representing the binocular visual field, even in species with laterally

positioned eyes. Stone (1983) hypothesized that the mammalian *area* may be the point of retinal fixation within the binocular field (Table 1, Hypothesis 4). Following Blakemore's (1969) hypothesis regarding bilateral representation of retinal neurons in the brain and studies of the distribution and central projections of individual ganglion cell types (Fukuda and Stone, 1974), Stone (1983) also suggested that X-cells subserve binocular depth discrimination at the fixation point. Given the small receptive fields, high cell density, and central projections of X-cells within the *area*, these cells will also facilitate high spatial resolution (see before and Cleland and Levick, 1974; Fukuda and Stone, 1974; Hughes, 1977).

Stone's (1983) hypothesis is supported by reports of a single afoveate *area* subtending a part of the binocular field in several species (Bloch and Martinoya, 1982; Collin and Pettigrew, 1988a; Collin and Partridge, 1996). After a quick review of the literature reporting retinal ganglion cell topography across all vertebrates, we found that 76% (109/144) of *areae* in species with a single *area* project into the binocular field, as determined from their position in the retina and estimates of binocularity based on eye position. For example, the laterally placed eyes of the coral cod *Cephalopholis miniatus* have a temporal *area* projecting into the binocular field (Collin and Pettigrew, 1989). However, out of the 144 species found to have a single afoveate *area*, 24% (35/144) do not project into the binocular field (eg, the Rufus snake eel *Ophichthus rufus*, Bozzano, 2003; the sleepy lizard *Tiliqua rugosa*, New and Bull, 2011). In species with multiple *areae*, the *areae* project to different parts of the visual field, suggesting that each specialized retinal region may be involved in more than just binocular fixation (Collin and Shand, 2003). For example, the teleost (*Navodon modestus*) possesses both temporal and nasal *areae*, which allow this fish to view the rostral (binocular) and caudal portions of their visual fields simultaneously with high acuity (Ito and Murakami, 1984; Collin and Pettigrew, 1988a). From our analysis of the literature, all 48 species found to possess multiple *areae* had at least one *area* projecting frontally subtending acute vision within the binocular field. This finding implies that although different *areae* may serve other functions, at least one *area* projects into the binocular region to facilitate binocular discrimination.

Bloch and Martinoya (1982) tested the visual acuity of the *area* in pigeons (*Columbia livia*) by behavioral means, and as a result proposed a new hypothesis, arguing that the dorsotemporal *area* of the pigeon was used for high visual resolution of close, stationary objects, but not for detecting distant and moving objects (Table 1, Hypothesis 5). In pigeons, discriminative ability decreased in the frontal field, which is subserved by the dorsotemporal *area*, as a function of distance but increased with distance in the fovea-mediated lateral field. Thus, the positioning of the *area* correlates with the part of the visual field that is used for viewing near versus far objects (eg, frontal or lateral fields). Electrophysiological studies supporting Bloch and Martinoya's (1982) hypothesis have shown that the *area* in the cat contains mainly brisk-transient retinal ganglion cells (Fukuda and Stone, 1974), which have slowly conducting axons and a preference for small, slow-moving objects (Cleland et al., 1973).

### 1.19.2.2 Radial Anisotropy

Radial anisotropy is a type of retinal specialization whose configuration is opposite to that of an *area*: instead of a concentric increase in retinal cell density toward a central point, there is a concentric increase toward the periphery of the retina (Fig. 1D). This type of specialization has been found in species with diverse types of eye placement in the skull: from more frontal in the South African clawed frog (*Xenopus laevis*) and the young burrowing frog (*Heleioporus eyrei*) (Dunlop and Beazley, 1984) to less frontal in the sawtoothed eel (*Serrivomer beani*) and the lanternfish (*Lampanyctus macdonaldi*) (Collin and Partridge, 1996).

Radial anisotropy has been hypothesized to provide higher acuity around the periphery of the visual field (Table 1, Hypothesis 6) (Dunlop and Beazley, 1981), where both food and/or predators may arise from any direction. Dunlop and Beazley (1981) also proposed that this specialization may function in movement detection (Table 1, Hypothesis 7), enabling the detection of objects moving into the visual field from any direction. Although the functional properties of radial anisotropy have not been tested empirically, the presumed benefit of higher resolution in the periphery is that individuals may have less need to move their heads or eyes to detect prey before capture. The tadpoles of the burrowing frog possess a radial anisotropy and live in aquatic environments, but this retinal specialization is lost as they mature and move onto land (Dunlop and Beazley, 1981). Considering this observation, plus the fact that several aquatic species have radial anisotropy, Dunlop and Beazley (1981) suggested that there may be an association between the presence of radial anisotropy and aquatic habitats.

### 1.19.2.3 Visual Streak

A visual streak was defined as a bandlike thickening across the retina in early ophthalmoscopic observations (Fig. 1C) (Chievitz, 1889, 1891; Slonaker, 1897). Closer examination using the light microscope revealed that this meridional thickening was comprised of high densities of retinal ganglion cells that formed a visual streak, suggesting a band of high acuity in the corresponding region of the visual field (Table 1, Hypothesis 8) (Hughes, 1977; Tancred, 1981; Fernández-Juricic et al., 2011; Lisney et al., 2013). The visual streak can be oriented in different positions within the retina. The most commonly observed orientation is horizontal, where the visual streak spans the retina parallel to the ground (or a horizon). However, several different degrees of inflection away from the horizontal plane have been found. Inflected streaks have been described in the Eastern chipmunk (*Tamias sibiricus asiaticus*) (Wakakuwa et al., 1985), the horse (*Equus ferus caballus*) (Guo and Sugita, 2000), the Florida garfish (*Lepisosteus platyrhincus*) (Collin and Northcutt, 1993), and the Canada goose (*Branta canadensis*) (Fernández-Juricic et al., 2011), and vertical streaks have been described in the two-toed sloth (*Choloepus didactylus*) (Costa et al., 1987), the African elephant (*Loxodonta africana*) (Stone and Halasz, 1989), the deep-sea bass (*Howella sherborni*) (Collin and Partridge, 1996), and the dromedary camel (*Camelus dromedarius*) (Harman et al., 2001).



The position of the visual streak depends on the position of the head of the animal. For example, the Canada goose has a visual streak oriented obliquely about 30 degrees from the horizontal plane when the head is parallel to the ground, but it can realign the streak with the horizon by tilting its head downward (Fernández-Juricic et al., 2011). Duijm (1958) argued that birds with an upwardly inflected visual streak would have the bill pointing downward as their usual head orientation (klinorhynch) so that the plane of the lateral semicircular canal, used for orientation in space, would be held horizontal. This would also result in a head position in which the visual streak is aligned with the horizon (Land, 1999; Lisney et al., 2013).

The visual streak is generally assumed to be involved in high-acuity vision, but it has also been hypothesized that this specialization may have more than one function depending on the populations of retinal ganglion cell types occupying the visual streak (Fukuda and Stone, 1974; Rowe and Stone, 1976; Table 1, Hypothesis 9). Although retinal ganglion cells of the brisk-sustained, X-cell type that would provide high resolution (Cleland et al., 1971) have a higher density in the visual streak than in the peripheral retina, they are not always the most abundant type of ganglion cell within the visual streak. In the cat, for example, the nasal extension of the visual streak has been shown both physiologically and morphologically to consist principally of W-cells (whereas X-cells predominate in the area) (Fukuda and Stone, 1974; Rowe and Stone, 1976). Ganglion cells of the W-cell type have slow-conducting axons and therefore may not be involved in high visual resolution. Furthermore, the receptive fields of the W-cells do not change in size across the retina (as compared to X-cells, whose receptive fields are smaller in the visual streak than in the periphery). This property may improve the ability of W-cells to detect small-moving objects at a distance, near the detection threshold of visual stimuli, without a substantial increase in the resolution of the image outline (Rowe and Stone, 1976). Therefore, Rowe and Stone (1976) hypothesized that, aside from an increase in visual resolution, the visual streak may also improve the detection of weak visual cues (Table 1, Hypothesis 10). However, the proposed functions of the visual streak have not been tested empirically, and the visual streak may have a range of functional properties based on the densities of different cell types within the streak and their central projections.

Based on the assumption that the visual streak mediates high-acuity vision, many ecological predictions have been made, relating the visual streak to the following: (1) the type of visual environment that a species inhabits, (2) the placement of the eyes in the head, and (3) an animal's visual ecology. Johnson (1901) first suggested that the presence of a visual streak is associated with grazing habits, a high risk of predation, and laterally placed eyes (Johnson, 1901; Vincent, 1912; Hughes, 1977). Prey species would benefit from a visual streak because it provides a wide field of view with high visual resolution, enabling them to better detect and track predators across the environment. Prey species in open habitats especially would benefit from a visual streak because, in such habitats, visualization of the environment is not obstructed. Laterally placed eyes also increase the spatial extent of the visual streak across the visual space due to a wider cyclopean visual field (binocular field + right and left lateral fields), further enhancing the benefits of having a visual streak. However, visual streaks have also been described in many predatory species, such as the spotted hyena (*Crocuta crocuta*) (Calderone et al., 2003), German shepherd (*Canis lupus f. familiaris*) and wolf (*Canis lupus*) (Peichl, 1992), and Tasmanian devil (*Sarcophilus harrisii*) (Tancred, 1981). This suggests that enhancing predator detection, or the association with grazing habits, may not be the sole function of a visual streak. Furthermore, eye placement may not be the sole reason for the presence of a visual streak, given the range of species with a visual streak, eg, some prey species with frontally placed eyes have a visual streak, including the Western gray kangaroo (*Macropus fuliginosus*) (Beazley, 1985) and the red kangaroo (*Macropus rufa*) (Hughes, 1975).

Vincent (1912) suggested that the visual streak may provide "panoramic vision" with high spatial resolution across the visual field. This configuration would allow animals to focus on large regions of visual space that may be of interest, particularly in terms of detecting predators (Tancred, 1981). Wood (1917) suggested that the widened field of high-acuity vision provided by the visual streak decreases the need for head movements while feeding, as the retinal region with high visual acuity is broad compared to the other retinal specializations. When an animal with a visual streak is static, its retinal specialization would project across a larger portion of the visual space, and therefore decrease the need to move the head to align the visual streak with a target of interest.

Pumphrey (1948) was the first to associate the visual streak with the horizon and hypothesized that birds of flight occupying open habitats in which the horizon dominates, such as the sea, desert, or grassland, should have a visual streak. This is consistent, for example, with studies of the Manx shearwater (*Puffinus puffinus*) (Hayes et al., 1991). Luck (1965), elaborated on Pumphrey's hypothesis stating that the horizon is an important source of information about both prey and predators and that species inhabiting horizon-dominated habitats should have a visual streak oriented horizontally (horizontal visual streak). Brown (1969) further extended this argument by suggesting that a visual streak should be present in species in which the head is held close to the ground. Brown (1969) strengthened this argument by revealing a streak in the retina of the red-eared turtle (*Pseudemys scripta elegans*) and to suggested that animals low to the ground would almost always view a horizon (provided by the ground near to them and either the sky or vegetative/environmental cover), where the streak could enhance both visual resolution and attention over an extended area. Yet, a visual streak persists in some species whose head is high relative to the ground, such as the ostrich *Struthio camelus* (Boire et al., 2001), African elephant *L. africana* (Stone and Halasz, 1989), horse *E. f. caballus* (Harman et al., 1999), and giraffe *Giraffa camelopardalis* (Coimbra et al., 2013).

Hughes (1977) took the association between the horizon and the visual streak a step further by proposing the "terrain hypothesis," which states not only that the presence of a visual streak is associated with a horizon-dominated environment, but also that the line of vision should not be obstructed by vegetation. Data from many species support the terrain hypothesis, such as the ostrich (Boire et al., 2001), the spotted hyena (Calderone et al., 2003), Western gray kangaroo (Dunlop et al., 1987), and wolf (Peichl, 1992). The terrain hypothesis has also been applied to aquatic vertebrates, as both the ocean floor and ocean surface provide an unobstructed horizon upon which a horizontal streak could be used to focus on with high visual resolution. For example, Collin

and Pettigrew (1988b) found that the blue tuskfish *Choerodon albigena*, red-throated emperor *Lethrinus chrysostomas*, and collared sea bream *Gymnocranius bitorquatus* all have a visual streak and live within an underwater environment where the sand–water interface provides a horizon as the primary visual landmark. However, many species have a horizontal visual streak but live in habitats with a visually obstructed horizon. For instance, the Australian frogfish *Halophryne diemensis* lives in caves and crevices yet possesses a weak visual streak (Collin and Pettigrew, 1989). The chameleon *Chamaeleo chamaeleon* (Hassni et al., 1997) and brush-tailed possum *Trichosurus vulpecula* (Freeman and Tancred, 1978) are both arboreal species with horizontal streaks, while the arboreal snake *Philodryas olfersii* possesses a visual streak, yet its open habitat terrestrial congener *Philodryas patagoniensis* does not (Hauzman et al., 2014).

The visual streak has also been suggested to aid in aerial navigation in birds (Pennycuik, 1960; Mathews, 1968). For example, Canada geese possess an inflected streak that may aid in the visualization of landmarks during migratory flights and/or be used to maintain flight pattern formation (Fernández-Juricic et al., 2011). Sometimes, while in their V-formation, Canada geese align themselves in a stair-step fashion, such that individuals above and in front of them, as well as below and behind them, can be viewed at high resolution (Fernández-Juricic et al., 2011). However, many birds possessing visual streaks do not fly in specific group formations, including the common diving petrel *Pelecanoides urinatrix* (Hayes et al., 1991) and the sooty albatross *Phoebastria fusca* (Hayes and Brooke, 1990). The visual streak has also been suggested to be a benefit to species that engage in long flights, such as the Manx shearwater, because long flights require greater maintenance of orientation and landmark visualization for the purpose of navigation (Hayes et al., 1991).

In some species, the presence of a visual streak cannot be easily explained with any of the aforementioned hypotheses. For instance, ungulates and elephants have a horizontal visual streak with an additional dorsotemporal extension, termed an anakatabatic area (Stone and Halasz, 1989; Schiviz et al., 2008; Pettigrew et al., 2010; Coimbra et al., 2013). The anakatabatic area is longer in taller ungulates, suggesting it may serve some function in locomotion because it is always directed toward the front hooves (Schiviz et al., 2008), but the visual streak in these species is of the same shape regardless of whether the habitat is horizon-dominated or not (Schiviz et al., 2008). Furthermore, dual visual streaks may provide wide high-resolution coverage in two spatial dimensions and may compensate for the limited degree of eye movements found in these species (Stone and Halasz, 1989). Another interesting example is the dromedary camel, which inhabits primarily deserts with an unobstructed horizon, yet possesses two vertical streaks, one nasally and one temporally (Harman et al., 2001).

#### 1.19.2.4 Fovea

The fovea is a type of retinal specialization with a pitted invagination of the retinal tissue (Chievitz, 1890; Slonaker, 1897). Foveae differ substantially in the depth of the pit from shallow (concaviclivate) to deep (convexiclivate). These two types have been further broken down into four morphologically distinct types (Collin and Collin, 1999; Collin and Shand, 2003). A type 1 fovea is a deep (convexiclivate) invagination of the retinal tissue without any lateral displacement of the inner retinal layers (ie, ganglion cell layer, inner nuclear layer, inner plexiform layer). Type 2 foveae are also deep invaginations, but there is lateral displacement of the inner retinal layers, which allows light to strike the underlying photoreceptors without having to pass through the extra retinal layers. A type 3 fovea is very similar to a type 2 fovea but includes a dense, darkly staining material and a thick fiber layer lining the inside of the pit that is thought to refract light (Henle fiber layer; Ohzu et al., 1972). Finally, a type 4 fovea is a shallow (concaviclivate) invagination that exhibits no lateral displacement or radial fibers (Collin and Collin, 1999).

When present, the fovea is the retinal region with the highest retinal ganglion cell density (or two highest regions if two foveae are present), and it often occurs within an *area* (Walls, 1942) or a visual streak (Fernández-Juricic et al., 2011). However, the very center of the foveal pit generally has a decreased (or zero) density of retinal ganglion cells due to the lateral displacement of the inner retinal layers. Distinguishing between fovea types is important because morphological differences will differentially affect the incident light striking this region of the retina before it reaches the photoreceptor layer. A recent study has proposed a new method to standardize the measurement of foveal pit morphology (depth and width) across different vertebrate species (Moore et al., 2016a).

The fovea is regarded as having the highest resolution of all retinal specializations (with deeper foveal pits having higher spatial resolving power) because of its high density of photoreceptors and retinal ganglion cells (Table 1, Hypothesis 11) (Inzunza et al., 1989; Ross, 2004). The superior resolution of the fovea in birds of prey, for example, can provide one of the highest visual acuities in vertebrates (Walls, 1942; Fox et al., 1976; Martin, 1986; Reymond, 1987; Gaffney and Hodos, 2003; Marmor et al., 2008). This high visual resolution hypothesis has been supported by behavioral experiments and by studies of different retinal components: photoreceptor properties, synaptic circuitry, optical properties of the foveal pit, reduction in vasculature and retinal tissue, etc. (Fox et al., 1976; Reymond, 1985, 1987; Martin, 1986; Gaffney and Hodos, 2003; Marmor et al., 2008; Potier et al., 2016). In the next paragraphs, we explain these components in detail.

Properties of the photoreceptors can affect the visual resolution mediated by the fovea. Elongated and more closely spaced outer segments (where light is absorbed) can capture more light and do so at a finer level of detail, and therefore gather more information at a finer resolution (Hughes, 1977). A lower ratio of photoreceptors to retinal ganglion cells (neuronal convergence) should also provide a more direct route of visual information to the brain and reducing synaptic noise (degradation of the physical image) (Fite and Rosenfield-Wessels, 1975).

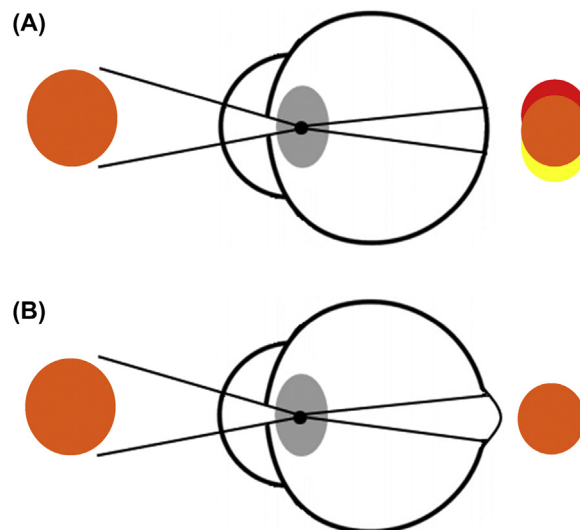
Rodieck (1973) attempted to explain the high resolution of the fovea by focusing on properties of the foveal photoreceptors that may reduce chromatic aberration (ie, the inability to focus all wavelengths of light at the same convergence point) (Table 1,

Hypothesis 12). Because chromatic aberration causes different wavelengths of light to be dispersed unevenly across the retina, focusing light over a broad spectral range can be challenging. Synthetic lenses, eg, in a camera, are made to correct for chromatic aberration by combining positive and negative aberration effects that can cancel each other out. However, if only a single lens is used (as in most vertebrate eyes), the aberration can be serious enough to cause colored “halos” around some image features. For example, when viewing the edge of a white object, the edge will not be seen as sharp but rather tinged with color (Thibos et al., 1990). The foveal pit tends to contain few S-cones (short wavelength-sensitive cones), which reduce the spectral range within the fovea and therefore probably reduce chromatic aberration (Fig. 3; Rodieck, 1973; Calkins, 2001; Ross, 2004). However, the reduction in chromatic aberration may only apply to animals with specific environment/visual lifestyles, as the densities of different types of photoreceptors (including S-cones) vary across species. Marmor et al. (2008) found that humans with foveal hypoplasia (lack of a foveal pit) retain the aforementioned foveal cone properties that allow patients to maintain high visual resolution. These examples suggest that photoreceptor properties play an important role in accounting for the high visual resolution of the fovea that may be independent of the pit itself.

The synaptic circuitry around the fovea is enhanced by a sharp increase in retinal ganglion cell density compared to the periphery of the retina, and thus an increase in visual resolution. This is accompanied by an increase in photoreceptor density (and hence neuronal convergence, as explained before). At the very center of type 2 and 3 foveae, retinal ganglion cells are completely displaced, facilitating the direct access of light to the photoreceptor layer. The circuitry of ganglion cell axons within different brain regions may also be important in the function of the fovea. For example, it has been shown that the temporal fovea in the American kestrel *Falco sparverius* projects via the thalamofugal pathway to the visual Wulst, which contains a representation of the binocular zone (Pettigrew, 1978; Frost et al., 1990). The thalamofugal pathway to the visual Wulst may mediate the fine conjugate eye movements used for binocular vision (Pettigrew, 1978), which are important when viewing close objects in the frontal field and perhaps for visual tasks that may benefit from high visual acuity afforded by the fovea (eg, during prey capture). This suggests that high visual resolution may be implicated in binocular vision in these species. However, a system such as this would only be used if the bird possesses some degree of stereoscopic depth perception (Frost et al., 1990), as shown behaviorally in American kestrels (Fox et al., 1977) and barn owls (van der Willigen, 2011).

The synaptic circuitry within the retina may enhance visual resolution at the fovea. For example, outside of a retinal specialization, ganglion cells receive information from many photoreceptors, acting as a bottleneck of information as the electrical signal is sent toward the brain (Collin, 1999). Accordingly, retinal cell density would be the primary limit to visual resolution. However, in areas of high cell density (within retinal specializations, particularly within foveae), ganglion cells may synapse with photoreceptors in a near 1:1 ratio creating a “private line” of communication (Dacey, 1993). Foveal specializations may then further enhance the visual resolution beyond what can be accomplished by the “private line” of neural sampling, where there is frequently an absence of rods that contribute largely to sensitivity rather than resolution thereby allowing for maximal density of cone photoreceptors that may contribute to resolution (Rossi and Roorda, 2010; Coimbra et al., 2015).

A few hypotheses attempt to explain the functional properties of the fovea based on the curvature and shape of the foveal pit. Specifically, it has been proposed that alterations of the light image created by the unique pitted structure of the fovea may enhance visual resolution compared to other retinal specializations (Rossi and Roorda, 2010). This hypothesis takes into consideration the



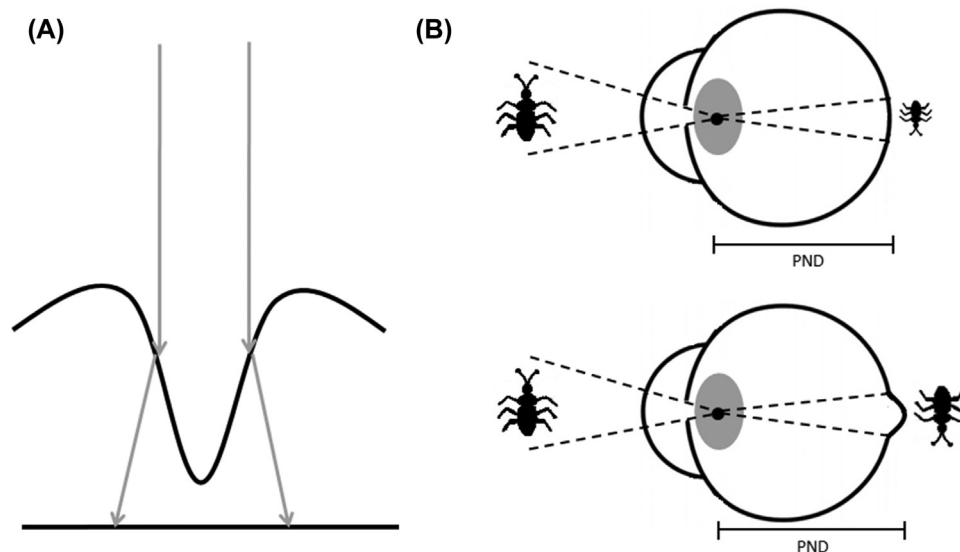
**Figure 3** Reduction of chromatic aberration by the fovea (Rodieck, 1973) (Table 1, Hypothesis 12). (A) In the absence of a fovea, different wavelengths of light of the image fail to be focused on the same convergence point on the retina making the image blurry. (B) When a fovea is present, wavelengths of light of the image are more tightly focused onto a single convergence point on the retina making the image appear sharp and without color “halos.”

refractive index of the vitreoretinal boundary (Walls, 1937; Snyder and Miller, 1978; Locket, 1992), reduction of light scatter due to clearing of retinal tissue (Walls, 1937; Weale, 1966), the steepness of the foveal pit walls, and the curvature at the bottom of the foveal pit leading to image distortion (Pumphrey, 1948; Bloch and Martinoya, 1982; Maldonado et al., 1988; Harkness and Bennett-Clark, 1978; Steenstrup and Munk, 1980; Locket, 1992).

Walls (1937, 1940, 1942) was the first to propose an optical hypothesis for the fovea suggesting that the deep convexiclivate foveal pit magnifies an image by two different methods. First, light is refracted upon striking the vitreoretinal boundary, as indicated by Valentin's (1879) measurements showing that the refractive index of the retina is higher than that of the vitreous humor (Table 1, Hypothesis 13) (Walls, 1942). Light going from the vitreous humor to the photoreceptor layer would be refracted outward expanding the image upon reaching the photoreceptors, thereby increasing visual resolution (Fig. 4A; Walls, 1942). Walls (1940, 1942) also considered the possibility of a shallow concaviclivate fovea magnifying the image, but suggested that the amount of refraction would not be enough to cause a significant increase in image magnification and, hence, visual resolution (Williams, 1980; Ross, 2004).

The second mechanism through which a deep fovea magnifies an image is by increasing focal length (from the cornea to the photoreceptors), which correlates with foveal pit depth (Walls, 1942). This increase in focal length is expected to be larger in deep foveae (Table 1, Hypothesis 13; Fig. 4B). Snyder and Miller (1977, 1978) expanded this idea by considering the anatomical resolving power (focal length/intercone spacing) in the fovea. They showed that avian deep foveae only have a slightly smaller intercone distance compared to shallow foveae in humans, likely because there is the possibility for "cross-talk" if photoreceptors are spaced too close to one another, reducing contrast sensitivity (Snyder and Miller, 1978). Snyder and Miller (1978) proposed the idea of a telephoto system at the bottom of the foveal pit (rather than focusing along the steep sloping walls), which is curved as if it were a negative lens that could act as a magnifier of the image. Anatomical measurements showed that the concavity of the bottom of the pit could theoretically increase the focal length beyond the axial length of the eye at the center of the foveal pit (Snyder and Miller, 1978; Locket, 1992; Collin and Shand, 2003). A similar idea was suggested for invertebrates (ie, jumping spiders within the family Salticidae; Williams and McIntyre, 1980). Snyder and Miller (1978) also used interference microscopy to show that the area beneath the foveal pit has a nonuniform refractive index, which is consistent with the base of the pit acting as a negative lens and magnifying the image. Yet, a negative lens can have disadvantages, such as yielding a narrower field of view with high resolving power and an increased susceptibility to aberrations caused by the sloping foveal walls (see Pumphrey, 1948).

Walls (1937) also hypothesized that the fovea reduces light scattering not only due to refraction at the vitreoretinal boundary but also within the fovea itself, due to the absence of overlying retinal tissue (Table 1, Hypothesis 14; Fig. 2). This idea was later formalized by Wolff (1940) and Martin (1986). They suggested that the morphology of the fovea reduces the number of retinal layers within the foveal pit, leaving a clearer path for the visual image to reach the photoreceptor layer, which would ultimately minimize refraction (Table 1, Hypothesis 14; Fig. 2) (Walls, 1937; Martin, 1986). However, early studies suggested that the retinal tissue is optically homogeneous and has near perfect clarity, implying that the degree to which it may scatter light is negligible (Walls, 1937; Weale, 1966). Weale (1966) discussed a simple experiment in which a ground glass of varying coarseness is placed opposite a visual acuity chart; he showed that the change in coarseness had to be large before any difference in visual acuity was noted. Subsequently,



**Figure 4** Image magnification caused by the fovea (Walls, 1942) (Table 1, Hypothesis 13). (A) Refractive differences between the vitreous and the retina cause the image to be magnified on the photoreceptor layer. Image modified from Walls, G.L., 1942. *The Vertebrate Eye and Its Adaptive Radiation*. Cranbrook Institute of Science, Michigan. (B) A fovea increases the posterior nodal distance (PND) and thus the size of the image on the retina.



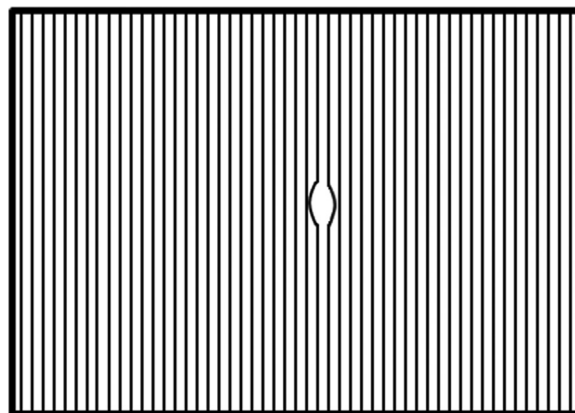
Weale (1966) suggested that the primary benefit of tissue displacement away from the fovea is that the retinal blood vessels are displaced, reducing light interference. However, some mammals lack retinal vasculature around their *area* but do not have a fovea (Walls, 1942; Rohen, 1966; Weale, 1966; Wolin and Massopust, 1970). Moreover, birds, which commonly have foveae (Wood, 1917; Meyer, 1977), do not have retinal vasculature at all, even in the retinal periphery. Therefore, if clearing of retinal tissue from the light path to the photoreceptors is the purpose of having a fovea, then perhaps the light scatter may not be due solely to retinal vasculature (Collin and Collin, 1988). However, previous studies have only considered the refraction of light as it crosses the vitreoretinal boundary and the curvature of the sloping sides of the foveal walls (Locket, 1992). The refractive properties of each retinal layer is yet to be determined. The retina is clearly a heterogeneous tissue, and the foveal pit may have a higher refractive index closer to the vitreous (Snyder and Miller, 1978; Locket, 1992). Further testing of refractive differences within the pit and throughout the retina itself would be important to better understand the effects of tissue clearing to minimize light scatter as a hypothesis to foveal function.

If the image is not exactly aligned upon the axis of symmetry with the fovea, the effect may not be of magnification but rather of distortion (Pumphrey, 1948). Based on modeling estimates, Pumphrey (1948) hypothesized that a deep fovea would be a good design for accentuating the angular displacement of light caused by the sloping foveal walls, and thus should be associated with movement detection, as an object fixated upon changes in eccentricity (a measure of the deviation from the normal shape) (Table 1, Hypothesis 15; Fig. 5) (Pumphrey, 1948; Locket, 1992). This property of a deep fovea would also allow fixation on moving objects as they approach the limit of visibility (eg, due to distance, size, or contrast against the background), because the distortion of the image on a sloping foveal wall would produce a point of reference on that object against the background (Pumphrey, 1948). For example, tracking a single moving object amidst many similar moving objects, eg, a single vertical line surrounded by many identical lines that are moving across the screen, is very difficult for us to visualize with our shallow fovea. However, a deep fovea is likely to provide a visual advantage at the cost of a small amount of visual acuity due to image distortion within the pit, in which the deep fovea may allow for both improved fixation and sensitivity to movement (Fig. 5; Pumphrey, 1948).

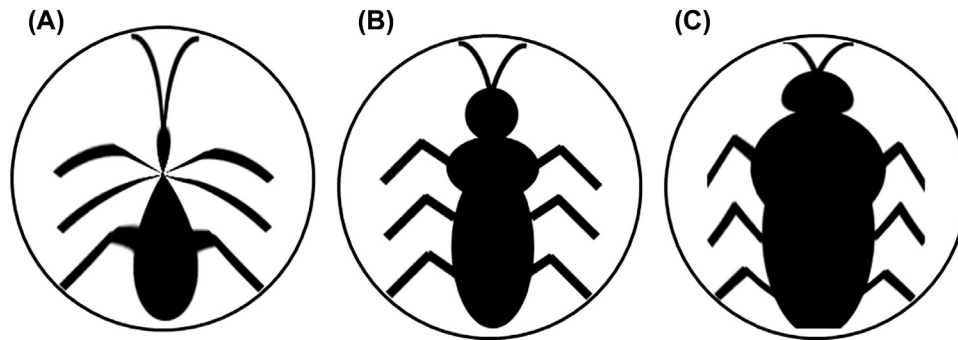
The hypothesis that the fovea is involved in movement detection has also been suggested for shallow foveae (Table 1, Hypothesis 15) (Maldonado et al., 1988). Bloch and Martinoya (1982) restrained pigeons and presented them with static, slow-moving, or fast-moving stimuli. The position of the bird's head was established from video recordings and fixation angles were then determined from the videos. The results revealed animals fixated with the lateral field when exposed to fast-moving objects, but fixated with the frontal field when exposed to slow-moving and static stimuli. This suggests that the shallow fovea of the pigeon is ideal for detecting fast-moving objects, whereas the dorsotemporal *area* of the pigeon is best suited for detecting slow-moving and static objects. Although the deep fovea was originally thought to provide sufficient distortion of the image to detect movement (Pumphrey, 1948), perhaps only a slight slope in the wall of the shallow foveal pit is required for the detection of movement, as movement detection is actually dependent on the distance to the object. However, there is no relationship between fixation accuracy and various foveal characteristics within humans (Wilk et al., 2016).

If the fovea does have a magnifying (Walls, 1937) or distorting (Pumphrey, 1948) effect on the image, then the more exaggerated slope of the deep fovea should have a greater effect than the low slope of the shallow fovea. Furthermore, the ability of the shallow fovea to detect movement or visualize items with high resolution is likely due to the corresponding projections to the brain (Schneider, 1969; Ingle, 1973; Karten et al., 1973; Lennie, 1980; Maldonado et al., 1988).

Harkness and Bennet-Clark (1978) hypothesized that the deep fovea can serve as a directional focus indicator (Table 1, Hypothesis 16, Fig. 6). They proposed that any refraction of light at the surface of a deep fovea can be considered negligible since it will only affect a small portion of the image, and the fovea may be a focus indicator because (1) the level of focus is more easily determined



**Figure 5** Distortion of a deep fovea as described by Pumphrey (1948) (Table 1, Hypothesis 15). As evenly spaced lines move across the screen, it is difficult to image a single line and track it across the screen with a shallow fovea (as in humans). However, if the deep fovea causes distortion of the image, it will be much easier to fixate and track the lines as they move across the screen. Figure modified from Pumphrey, R.J., 1948. The theory of the fovea. *J. Exp. Biol.* 25, 299–312.

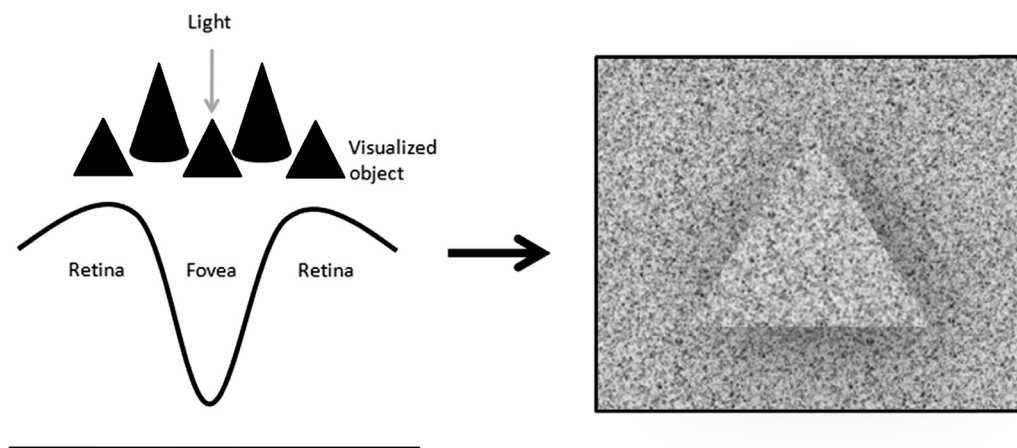


**Figure 6** Schematic of how the fovea can act as a sensitive, directional focus indicator (Harkness and Bennet-Clark, 1978) (Table 1, Hypothesis 16). (A) The image is focused in front of the object causing “pinhole distortion.” (B) The image is focused on the object. (C) The image is focused behind the object causing “barrel distortion.”

when the information is gathered from a small portion of the visual field (the foveal pit) and (2) the area of the image distorted by the fovea (see Pumphrey, 1948) lies at the center of the part of the visual field viewed in high resolution, which is the ideal for monitoring the focus of the image (Toates, 1972; Harkness and Bennet-Clark, 1978). Harkness and Bennet-Clark (1978) showed that for monocular animals (ie, animals with lateral eyes and no binocular overlap), the deep fovea might provide a special system for indicating focus. They modified a camera lens by applying nail varnish and creating a pinhole depression to represent the fovea. Viewing a graticule through this “fovea” of the camera they focused an image either on a plane beyond the object (behind the fovea) or on a plane closer to the camera than the object (in front of the fovea) (Snyder and Miller, 1978); each scenario produced a different type of distortion. Since the distortion of the image differed depending on where the image was focused, the distortion produced by the fovea may provide a focus indicator (Snyder and Miller, 1978).

Locket (1992) showed that an image at a given position on the retina (eg, perifoveal or areas just outside the fovea) can be accommodated by the lens and thus be in focus. However, he also suggested that different degrees of lens accommodation may be necessary to focus an image falling upon the multiple portions of the retina (eg, the fovea and perifoveal areas) due to variations in the posterior nodal distance in these retinal areas. Thus, when the image is in focus in the pit of a deep fovea, it may be out of focus in the perifoveal area, and vice versa (Locket, 1992). The level of focus is dependent on the *f*-number (focal length/diameter of the pupil). As the *f*-number decreases, the depth of focus is restricted to fewer planes. For example, if an animal has a very small pupil (or a very long focal length) and thus a large *f*-number, the difference in focus between the center of the fovea and the perifoveal areas will be negligible. Conversely, it has been shown in electrophysiological refraction studies that birds can focus near objects with their dorsal retina and distant objects with their lower retina simultaneously (Fitzke et al., 1985; Hodos et al., 1985; Hayes et al., 1987; Maldonado et al., 1988).

Steenstrup and Munk (1980) hypothesized that, if the axis of both the left and right foveae falls upon the same point within the binocular visual field, the image falling on the walls of each fovea (ie, everywhere except directly on the center of each fovea) may produce a skewing of that image in the same direction in both eyes (Table 1, Hypothesis 17; Fig. 7) (Steenstrup and Munk, 1980;



**Figure 7** Representation of how when an image (triangle) passes from the perifoveal region of a convexiculate fovea onto the sloping foveal wall, the image may be skewed. The skewing of a camouflaged image against its background may aid in the breaking of camouflage (Steenstrup and Munk, 1980) (Table 1, Hypothesis 17).



Locket, 1985, 1992; Wagner et al., 1998). Using ray plotting, Locket (1992) showed that the image would be magnified when centered on the foveal pit but skewed by distortion when the image is off-center (falling on the foveal walls). For example, as part of an image passes from outside the fovea to the foveal pit, the portion of the image inside the pit would be skewed, separating the object visually from the background. This special optical effect could aid animals in capturing prey in optically empty space (a featureless environment that does not provide other visual objects as a spatial reference for depth perception) or in the breaking of camouflage (Steenstrup and Munk, 1980; Locket, 1985, 1992; Wagner et al., 1998). The skewing of the image may further aid in breaking camouflage if the cone mosaic contains many double cones, because the skewed image passing across a double cone is likely to stimulate only one of the neighboring double cones (Steenstrup and Munk, 1980). The uneven stimulation of the cone mosaic would cause variation in the stimulation of different parts of the visual image (eg, between potential prey and the background) (Steenstrup and Munk, 1980). Breaking camouflage with the fovea can be a useful strategy for birds of prey, for example, as they search for prey from a distance (either in flight or perched) with their deep fovea projecting into the lateral, monocular field (Tucker, 2000). It may also be important in deep-sea fishes because these species have an optically empty environment in which there is no available visual background reference for depth perception (Locket, 1992).

All previous hypotheses have considered only parallel rays of light emanating from a hypothetically infinite viewing distance. However, nonparallel light rays entering through the pupil at different angles may have different effects from those previously mentioned. If nonparallel light rays strike the vitreoretinal boundary, the image may be magnified or distorted to varying degrees because the light rays will arrive at the vitreoretinal boundary at different angles and therefore refract at different angles. Further testing of different paths of light rays falling on the fovea may reveal more beneficial optical properties given by a fovea.

Finally, the fovea may be more closely related to an *area* than previously thought despite having a structural invagination and apparent optical effects. As previously mentioned, similarities revolving around photoreceptors have been documented (afoveate humans, Marmor et al., 2008; canine cone bouquets, Beltran et al., 2014). Furthermore, Yarczower (1964) found that the fovea might not be providing a spatial discrimination advantage, because after a lesion of the central fovea, pigeons have almost no detectable change in spatial discrimination (Maldonado et al., 1988). Interestingly, the area of highest spatial discrimination in the pigeon is not in the lateral, fovea-mediated visual field, but rather the lower frontal, *area*-mediated visual field (Bloch and Martinoya, 1982, 1983; Bloch et al., 1984; Maldonado et al., 1988). In humans, word recognition in the foveal visual field is superior, after accounting for stimulus size differences, only if the sentence had meaning (Latham and Whitaker, 1996). These results suggest that the fovea may be similar to a retinal *area* in regard to visual acuity. This supports the idea that perhaps the fovea subserves multiple functions, including movement detection and high resolution at long distances, as demonstrated in pigeons (Querubin et al., 2009; Hayes and Holden, 1983; Miceli et al., 2006; Gunturkun and Hahmann, 1999; Rounsley and McFadden, 2005).

### 1.19.2.5 Area Gigantocellularis

As previously mentioned, there are several different types of retinal ganglion cells (Rodieck, 1973; Hayes et al., 1991; Field and Chichilnisky, 2007). Because of their size and relatively straight forward morphological recognition, one type, the giant retinal ganglion cells, has been studied more than other cell types. These cells are characterized by their large soma, extensive dendritic fields, and terminal stratification within several levels of the inner plexiform layer (Wässle et al., 1981; Hayes et al., 1991). Giant retinal ganglion cells have large receptive fields, which allow for the integration of more synaptic inputs (ie, high spatial summation), thereby providing high sensitivity but at the expense of spatial resolution (Reuter and Peichl, 2008).

Many studies have shown that the proportion of different types of retinal ganglion cells varies in different parts of the retina (eg, Provis, 1979). For instance, retinal ganglion cell size normally decreases with increased density toward the retinal specialization, possibly due to packing constraints (Stone and Keens, 1980; Wässle et al., 1981; Tancred, 1981). This may be one of the reasons why giant retinal ganglion cells are restricted to the retinal periphery in some species (Stone and Keens, 1980; Tancred, 1981; Inzunza et al., 1991; Collin and Shand, 2003). Giant retinal ganglion cells have been shown to project into the frontal, binocular field in lateral-eyed animals such as Eastern chipmunks (Wakakuwa et al., 1985) and North American opossums *Didelphis virginiana* (Rapaport et al., 1981). Both species have a dorsotemporal area gigantocellularis corresponding to the location where they grab and handle food items (Wakakuwa et al., 1985). A similar configuration has been found in Manx shearwaters (Hayes et al., 2001), domestic chickens *Gallus gallus domesticus*, pigeons, and quails *Coturnix coturnix* (Campaña and Suburo, 1981).

Additionally, the giant Y-type (or alpha) retinal ganglion cells of in the retina of multiple species have been found to be motion sensitive, both behaviorally (Hayes et al., 1991; Bailes et al., 2005; Coimbra et al., 2006) and electrophysiologically (Boycott and Wässle, 1974; Cleland et al., 1975; Peichl and Wässle, 1981). They are distributed throughout the retina in a relatively constant ratio with smaller ganglion cells (W-cells), as in the cat (Wässle et al., 1975).

Hayes et al. (1991) first termed a specialized region consisting of a high proportion of giant retinal ganglion cells as an area gigantocellularis. They hypothesized that the area gigantocellularis in procellariiform seabirds is used in movement detection (Table 1, Hypothesis 18) based on previous studies of the properties and distributions of giant retinal ganglion cells in mammals (Tancred, 1981; Boycott and Wässle, 1974; Cleland et al., 1975; Peichl and Wässle, 1981) and on correlations between the behavior of the seabirds and the position of the area gigantocellularis and which part of the visual field it subtends. For example, in the Manx shearwater, the area gigantocellularis projects just below the bill, which would aid these birds in catching fish below the surface while in flight.

Although an area gigantocellularis has been described in several species across various taxa, the functional significance of this retinal specialization is usually assumed to be the same as that of the giant Y-type retinal ganglion cells in mammals

(ie, motion detection). Specific regions of large ganglion cells have been found in the Australian lungfish *Neoceratodus forsteri* (Bailes et al., 2005), the Japanese catshark *Scyliorhinus torazame* (Muguruma et al., 2013), and the sturgeon *Acipenser transmontanus* (Bailes et al., 2005; Collin et al., 1998; Ito et al., 1999; Uemura et al., 2000; Hirt and Wagner, 2005), but no functional testing has been conducted. Additionally, the yellow-bellied elaenia *Elaenia flavogaster* and the mouse-colored tyrannulet *Phaeomyias murina* both have a dorsotemporal area gigantocellularis that projects into the frontal–inferior visual field and has been suggested to be involved in both movement detection and depth discrimination (Coimbra et al., 2009). Several deep-sea fishes, such as the bigfin pearleye *Scopelarchus michaelisarsii* (Collin et al., 1998) and the daggertooth *Anotopterus pharaoh* (Uemura et al., 2000), possess a temporal area gigantocellularis. The function of giant ganglion cells in these nonamniote species is unknown, but they have been suggested to also play a role in enhancing sensitivity in deep water with low levels of ambient light (Table 1, Hypothesis 19) (Stell and Witkovsky, 1973; Collin, 1988; Bozzano and Catalan, 2002; Bailes et al., 2005).

### 1.19.3 Future Directions

Most hypotheses regarding the function(s) of retinal specializations have revolved around cell distribution and the assumption that high cell densities provide high visual resolution, in some cases associated with specific habitat types. It is critical to test the functional properties of the cell types within these specializations, as well as the central projections of the different retinal ganglion cell types. However, the only way to infer what an animal is looking at is to study its behavior (Tucker, 2000). More specifically, we need tests that assess the visual behavior of the animal in relation to specific parts of the retina. Taking advantage of past electrophysiological and axonal tracing methods to determine cell function and central projections, and novel technologies (eg, eye trackers) to study visually guided behavior, we can design empirical tests of how animals use their retinal specializations to explore their surroundings by manipulating their visual space.

Another set of hypotheses have been constructed around the optical effects that some retinal specializations may confer. Although many of the functional properties of the retinal specializations have been tested to some degree (Table 1: behaviorally 6/19, optically 5/19, physiologically 4/19), there may be other ways to test the same hypotheses using different methods or technological advances. Sophisticated optical equipment [eg, adaptive optics, lasers, holographic interferometers, optical coherence tomography (OCT)] may help to clarify the many optical properties of the retinal specializations.

We have classified testing the functional properties of retinal specializations based on four different types of approaches: behavioral, cell type, optical, and developmental and genetic.

#### 1.19.3.1 Behavioral Approaches

The *area*, visual streak, and fovea have all been proposed to be involved in high-resolution vision (for visual search and visual fixation purposes). Therefore, we would expect animals to align these retinal specializations with objects of interest. Because the density of photoreceptors and ganglion cells is not homogeneous across the retina, this alignment occurs mostly through head and eye movements. One way of testing this hypothesis is to compare head/eye movement behavior between baseline (ie, no object of interest in the environment) versus visual target (ie, object of interest present in the environment) conditions. In the baseline conditions, animals are expected to move their eyes/heads randomly and at relatively high rates and amplitudes as they would be visually exploring the environment (Dunlap and Mowrer, 1930; Friedman, 1975; Fernández-Juricic, 2012; Land, 2015). In the visual target conditions, animals are expected to concentrate their head positions around the object of interest and move their eyes/head at relatively slower rates and amplitudes due to visual fixation (ie, keeping gaze on a particular location of visual space). In the visual target conditions, animals can be exposed to different objects (eg, prey, predators, conspecifics, heterospecifics). Additionally, objects can be positioned at different distances to challenge visual resolution: a reduction in the detail of the object would enhance fixation-directed behavior.

Some species rely more on head movements (eg, birds: Steinman, 1973; Land, 1999, 2015; but see Tyrrell et al., 2015), while others rely more on eye movements (eg, most primates: Walls, 1942; Duke-Elder, 1958; Martin, 1988; Land, 1999, 2015). For example, in some bird species such as great horned owls *Bubo virginianus* (Steinman, 1973), eye movements are restricted due to eye shape and the tight fit of the eye within the orbit (birds in general tend to have smaller extraocular muscles relative to eye size than mammals; Jones et al., 2007; Land, 1999, 2015). In species that rely mostly on their head to align the retinal specialization with objects of interest, we can determine targets of visual attention by recording the patterns of head movements as objects in the visual space are manipulated. Such studies have been performed in barn owls (Ohayon et al., 2006), chickens (Dawkins, 2002), and pigeons (Hamilton and Goldstein, 1933; Chard, 1939; Blough, 1971, 1973; Hodos et al., 1976; Hodos and Leibowitz, 1977; Bloch and Martinoya, 1982).

In species that rely mostly on eye movements, recent advances in eye-tracking technology (primates, Machado and Nelson, 2011; dogs, Williams et al., 2011; birds, Yorzinski et al., 2013; Tyrrell et al., 2014) make it possible to understand to which part of the visual field the retinal specialization is directed (ie, center of visual attention). The technology consists of two cameras; one is positioned facing the animal's eye (eye camera) directed toward the center of the pupil, and the other camera is positioned above the head capturing the image of the visual space from the animal's perspective (scene camera). Calibration of the two cameras is performed as the animal visually acquires fixed images in space (dots set in a specific place), in which the distance between the point

and the animal is fixed to maintain calibration (Williams et al., 2011). Both camera views are then visualized on a computer, with a dot of reference showing where the retinal specialization is moving.

Although head and eye tracking are becoming technologically possible, it is essential to emphasize that, for these studies to work, the technology has to be calibrated for the retinal topography of the model species (eg, Tyrrell et al., 2014). For instance, eye-tracking technology relies on tracking the position of the pupil, which is generally associated with approximately the center of the retina. However, if the *area* or fovea of a species is located temporally, for example, then the interpretation of the eye tracker data may be erroneous. Consequently, it is necessary first to map out the density and distribution of retinal cells to establish the exact position and number of the retinal specializations (see Moore et al., 2012). This information can then be used to calibrate the eye-tracking software based on the position of the pupil (which is assumed to be at the center of the eye).

Eye-tracking technology would also be useful for testing whether the deep fovea (Pumphrey, 1948), shallow fovea (Bloch and Martinoya, 1982), and area gigantocellularis (Hayes et al., 1991) are used for image fixation or motion detection (Table 1, Hypotheses 13, 16, 19). We predict animals presented with moving objects (eg, on computer screens or under visually controlled conditions) would use their retinal specialization(s), rather than other parts of the retina, to scan the environment for moving objects (Tyrrell et al., 2015). With this method, threshold object speeds for object detection and recognition can be determined in species with different types of retinal specializations.

Eye-tracking technology would also be a useful approach for testing the hypothesis proposed by Steenstrup and Munk (1980), ie, that the fovea could be used to break camouflage (Table 1, Hypothesis 15). The technology should allow us to examine whether an animal positions its fovea on the cryptic item or on the background, and whether the animal follows a specific pattern of fixation (ie, fixation duration, number of fixations, etc.) before a correct foraging event.

Testing the function of a visual streak may be especially challenging. The fact that this retinal specialization occupies a larger portion of the retina limits the usefulness of eye-tracking technology, mainly because it is unclear which part of the large visual streak should be used for calibration. Studies on head movement (assuming limited eye movement) may shed more light on the function of the visual streak. By placing an animal with a visual streak in a synthetic environment with constructed backgrounds (ie, tilting of the horizon or various landscape features), we may observe changes in head orientation that indicate the baseline position of the visual streak (eg, horizontal plane in horizon-dominated environments, vertical plane in forests, etc.; Table 1, Hypothesis 8). Additionally, vision altering devices (eg, contact lenses, goggles) that blur different portions of the visual streak could lead to compensatory head movement strategies, thereby enhancing our understanding of the function of the visual streak.

The function of radial anisotropy in movement detection (Dunlop and Beazley, 1981) could be tested behaviorally (Table 1, Hypothesis 7). First, measuring the visual field of a given species, ie, using ophthalmoscopic reflex or electroretinography techniques (Fite, 1973; Grobstein et al., 1980; McComb and Kajiura, 2008; McComb et al., 2009; Martin, 2009), would establish the peripheral limit of visual space that the animal can see. Since radial anisotropy lies in the periphery of the retina, one can determine where the area of highest acuity is around the head. Second, conducting the types of behavioral experiments mentioned before (ie, no object vs object of interest in different parts of the visual field) would make it possible to identify changes in body orientation and behavioral responses (ie, attack prey, escape) that could be associated with specific visual traits (eg, visual resolution, motion, etc.).

### 1.19.3.2 Cell Type-Based Approaches

The huge diversity of retinal ganglion cell types associated with specific functions (Field and Chichilnisky, 2007) is underrepresented in most functional tests of retinal specializations. A few hypotheses have suggested specific functions for different cell types within the retinal specializations and their projections to visual brain centers (Blakemore, 1969; Fukuda and Stone, 1974; Rowe and Stone, 1976; Tancred, 1981; Hayes et al., 1991; Rahman et al., 2006). However, most of the literature on different vertebrate taxa is based on the distribution of all retinal ganglion cell types grouped together. To overcome this limitation, it is necessary to determine the distribution and function of different retinal ganglion cell types (Rowe and Stone, 1980; Cook and Chalupa, 2000). Rowe and Stone (1980) suggested neuron classification be based on not only cell distribution and morphology, but also axonal conduction velocity, central projections, receptive field size, and other receptive field properties. These criteria, along with the synaptic circuitry for each retinal ganglion cell, in different parts of the retina (and consequently the visual field), will bring new opportunities for behavioral experiments that measure head and eye position responses.

For example, the giant cells in the area gigantocellularis of the pearleye (Collin et al., 1998) and the daggertooth (Uemura et al., 2000) appear morphologically identical, but they have different physiological properties. The pearleye has mostly ON-center cells (ie, increase firing rate with central stimulation, decrease firing rate with peripheral stimulation), whereas the daggertooth has mostly OFF-center cells (ie, decrease firing rate with central stimulation, increase firing rate with peripheral stimulation). The former may help the deep-sea pearleye visualize bioluminescence against a dark background, whereas the latter should allow the daggertooth to visualize silhouettes against light backgrounds (Collin et al., 1998; Collin and Shand, 2003). Overall, understanding the distribution of different types of retinal neurons would enable much stronger predictions about how animals are visually and behaviorally interacting with their environment (Pushchin and Karetin, 2009).

Unfortunately, establishing cell types can be challenging. For example, electrophysiological testing of the retinal ganglion cells in the *area* of cats showed that 60% of the peripheral receptive fields were brisk-transient cells (alpha-type) (Cleland and Levick, 1974), whereas only 3% (Wässle et al., 1975) were of the alpha-type based on histopathological studies (Cleland et al., 1975; Hughes, 1977). Recent advances in adaptive optics may provide a way to test individual cell functions, while eliminating the problems associated with electrophysiology. For instance, microscopic control of a retinal stimulus using adaptive optics enabled Hofer et al.

(2005) to stimulate single cone photoreceptors in humans and showed that photoreceptors were responding to up to seven different established categories of color stimuli (Hofer et al., 2005; Roorda, 2011). This suggests that the function of a single cone photoreceptor depends not only on its wavelength absorption properties but also on its position in the retinal field with respect to other cone types (Brainard et al., 2008; Roorda, 2011).

One way of testing the functional properties of single cells is to use an adaptive optics scanning laser ophthalmoscope (AOSLO), which provides excellent control of the retinal stimulus and its placement and improves contrast and resolution when compared to past scanning laser ophthalmoscopes (Roorda, 2011). For instance, Sincich et al. (2009) used AOSLO to optically stimulate single cone photoreceptors, while simultaneously recording electrophysiologically from the corresponding neurons in a living animal (Sincich et al., 2009; Roorda, 2011). This is a promising technology, as such fine-tuned measurements would enable careful and accurate study of very small retinal areas that have thus far been largely neglected (eg, the fovea) (Roorda, 2011).

### 1.19.3.3 Optical Approaches

Most hypotheses regarding the function of the fovea are focused on its optical properties, particularly regarding the deep, concavitate foveae (Table 1, Hypotheses 11–15, 17–18). Testing the functional difference between the shallow and deep foveae would be important, but first it is necessary to establish a way of quantifying the steepness of the foveal walls, and the depth and width of the foveal pit. One approach is to use histological cross sections of the eyes of euthanized animals, but for some species, this is not an option. OCT can be a good alternative because it provides a visualization in vivo of cross sections of the retina, the optic nerve, and even individual cells (Tanna et al., 2010). OCT can be particularly useful to study the optical properties of the fovea because of the possibility of 3D reconstruction of the foveal pit, which would be very difficult to accomplish with a cross-sectional approach (Chalam et al., 2010; Dubis et al., 2009; Ruggeri et al., 2010). OCT has already made significant contributions to understanding different diseases that affect the fovea in humans (eg, Folgar et al., 2014; Garcia-Martin et al., 2014; Colombo et al., 2015).

Multiple optical hypotheses about the function of the fovea have been proposed (see Table 1). We may be able to test these by means of two different methods. First, to determine the effect of the optical properties of the fovea on the retinal image (ie, whether it distorts/magnifies the image or maintains its integrity after passing through the retinal tissue), it is possible to project a small collimated beam (ie, light rays that are nearly parallel, ideally not dispersing with distance) through the retina and examine the pattern of light that is reflected. If the exiting beam of light has the same diameter as the incident beam, then the retina maintained the integrity of the image as it was passing through. However, if the beam of light increases in diameter (ie, there is scatter), the fovea is distorting the image. Second, one can use an interferometer to remove any interference due to corneal/lens optics. Holographic interferometry emits a laser beam that is coherent, split into two paths, and then recombined in the eye (Williams, 1980). This technique can detect deformations in the recombined, single-wavelength beams, allowing us to compare image degradation in different areas of the retina (eg, fovea vs periphery).

The fovea of some species has been shown to possess a low number of S-cones, potentially reducing chromatic aberration (Rodieck, 1973; Calkins, 2001; Ross, 2004). Rynders et al. (1995) proposed that the magnitude of transverse chromatic aberration (ie, chromatic differences in position and magnification rather than focus, which is longitudinal chromatic aberration) varies linearly across the retina, and it is approximately zero at a single locus called the achromatic point. The achromatic point is dependent on the position of the optic axis (ie, the axis through the center of the cornea and lens), which is normally aligned with the visual axis (eg, fovea in the human) (Bradley, 1992; Rynders et al., 1995). However, the optic axis does not always fall on the fovea (eg, in species with multiple foveae) and therefore, depending on the position of the pupil, the chromatic aberration may be higher in these cases since the image falls outside the achromatic point (ie, no transverse chromatic aberration). Developing a method to test the level of transverse chromatic aberration across the retina at specific points [or by using current methods such as adaptive optics and wavefront sensing among other as described in Vinas et al. (2015)] may allude to whether or not the fovea helps in reducing the aberration effect. For example, if the transverse chromatic aberration is lower at the fovea than at other points within the retina, the fovea likely is an effective means of reducing transverse chromatic aberration (rather than being a consequence of the pupillary position or the waveguide properties of cone photoreceptors) (Rynders et al., 1995). Another test that could provide evidence that the fovea is reducing chromatic aberration would be to characterize the position of different types of cone photoreceptors within the foveal pit with different microscopic techniques. For example, a wide-spectral representation of cone photoreceptors in a deep fovea would require differential placement of cone types in different focal planes along the banking walls of the foveal pit.

### 1.19.3.4 Developmental and Genetic Approaches

Another way of testing the functional properties of the retinal specializations is to compare animals with and without those specializations in terms of both their development and genetic underpinning. For example, one may knock out some of the genes coding (eg, Bernstein et al., 1996; Kozulin et al., 2009) for different components of the retinal specialization (eg, pitted structure of the fovea, spectral sensitivity of photoreceptors, etc.), perhaps using some model organism. Marmor et al. (2008) showed that in humans with foveal hypoplasia (ie, lack of a foveal pit), foveal cone specializations remained normal, leaving acuity largely unaffected.

Developmentally, we can test the function of different retinal specializations, for example, by rearing wild and knock-out individuals in different types of visual environments (featureless, containing horizontal or vertical visual landmarks, containing



complex visual patterns, etc.). Would the animals still develop the retinal specialization with the same degree of functionality despite not being exposed to different visual stimuli during development? A mismatch would provide important cues as to the relevance of certain retinal traits during development or whether these traits are genetically programmed.

### 1.19.4 Conclusion

Many hypotheses have been proposed on the function of retinal specializations and their role in the visually guided behavior of animals, but empirical testing of these hypotheses has lagged. Consequently, little is known about the functional properties of retinal specializations in different vertebrate taxa. This has limited our understanding of the diversity of strategies animals use to gather visual information from different environments, and it has slowed our progress in mapping the functional evolution of vertebrate eyes. By focusing future research efforts on testing these functional hypotheses, we will be able to better comprehend the relationship between the eye and the physical environment, and ultimately the visual ecology of vertebrates.

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