

Brain Behav Evol 1990;35:85-97

## Correlation between Histological and Behavioral Measures of Visual Acuity in a Zooplanktivorous Fish, the White Crappie (*Pomoxis annularis*)

Howard I. Browman<sup>a</sup>, William C. Gordon<sup>b</sup>, Barbara I. Evans<sup>c</sup>, W. John O'Brien<sup>a</sup>

<sup>a</sup> Department of Systematics and Ecology, University of Kansas, Lawrence, Kans.;

<sup>b</sup> Department of Ophthalmology, Lions Eye Research Center, Louisiana State University Medical Center, New Orleans, La.;

<sup>c</sup> Institute of Neuroscience, University of Oregon, Eugene, Oreg., USA

**Key Words.** Visual acuity · *Pomoxis annularis* · Retina · Search behavior · Teleost · Terrain theory

**Abstract.** Estimates of visual acuity in a pelagic freshwater zooplanktivorous fish, the white crappie (*Pomoxis annularis*, Centrarchidae), were made using a behavioral measure, the maximum observed prey pursuit distance (MxPD), and a histological measure, the density of cone cells in the retina. The greatest number of pursuits occurs in the 0–30° wedge of the visual field; 87% of all pursuits occur in the first 40°. The longest pursuits (200 mm) also occur in this area and generally get shorter from 0 to 180° (from forward-directed) in the visual field. Consistent with the behavioral results, the largest number of cone photoreceptors (13,000/mm<sup>2</sup>) is found in the far temporal retina along the eye's horizontal meridian. Cone cell densities in the corresponding region of the nasal retina are approximately half this value. The number of cones decreases dorsally and ventrally from the horizontal meridian.

Although the absolute values of visual acuity calculated from cone cell topography (i.e. MxPDs of 500 mm) are 2–3 times greater than those observed behaviorally (i.e. MxPDs of 200 mm), the trends in visual acuity across the visual field obtained from both measures are consistent. We suggest that overestimates of visual acuity obtained from cone cell counts alone result from this measure's not accounting for, among other properties of the nervous system, cone cell convergence onto ganglion cells and higher brain centers. Behavioral measures of visual acuity are, therefore, likely to yield a more accurate estimate of an animal's visual abilities.

### Introduction

Teleost fishes exhibit a range of behavior rivaling that of birds and mammals. Many of these behaviors are visually guided, and both color and form are important in fish perception [e.g. Herter, 1953; Douglas and Djamgoz, 1990]. While sensitivity to line separation, wavelength interval and contour angle may be slightly less than in more visually advanced animals, similar processes of feature extraction and synthesis are likely to exist in fishes [Guthrie, 1983; Fernald, 1989; Douglas and Djamgoz, 1990].

Estimates of visual acuity in fishes have been made from both behavioral and histological parameters. In zooplanktivores, a fish's ability to locate prey has commonly been assessed by measuring its 'reaction' or 'pursuit distance' to specific prey under particular environmental conditions [reviewed in O'Brien, 1979; Lazzaro, 1987]. Reaction distance is defined as the distance between predator and prey at which the predator first 'notices' or reacts to the prey. Pursuit distance is operationally defined as the distance of the repositioning movement that precedes an attack on a prey item. These two measurements yield similar, but

## SEARCH SPACE

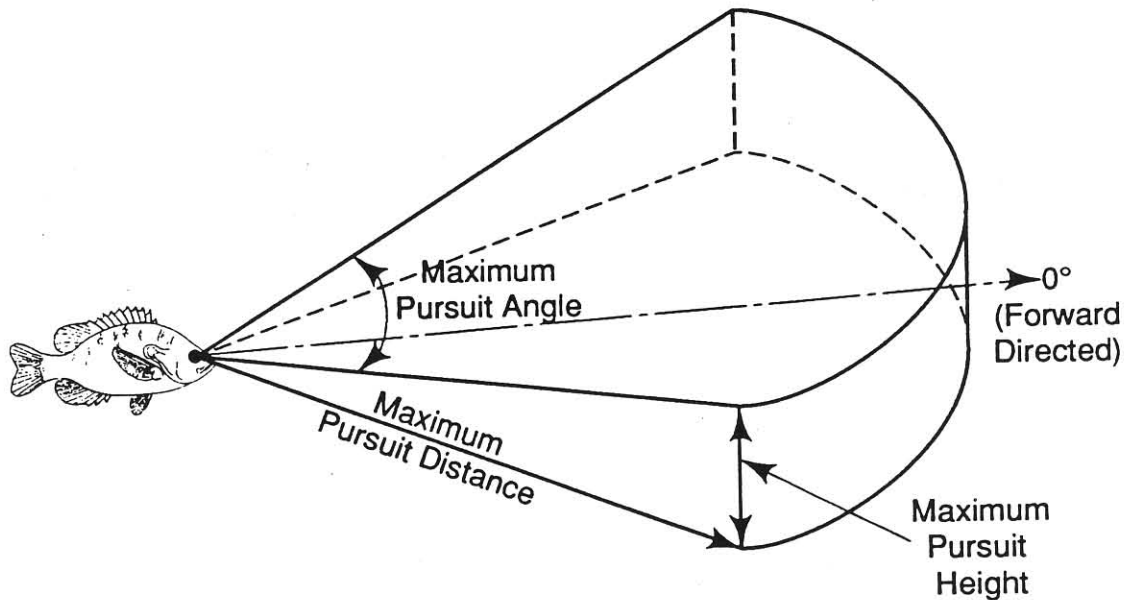


Fig. 1. Dimensions of a generalized search space as measured for the white crappie (*P. annularis*). The maximum pursuit angle, distance and height define the limits of the animal's acuity and the dimensions and geometry of the search space. Contrary to what is depicted in this illustration, the outer boundary of the search space varies across the visual field.

not identical, results. Typically, in feeding experiments carried out under a variety of conditions (light intensity, turbidity, prey type and/or size), many measurements of reaction of pursuit distance are made. Mean reaction or pursuit distances at various angles within the visual field are then used to define the limits of the fish's search space (fig. 1) [O'Brien, 1979; Lazzaro, 1987; O'Brien et al., 1990]. This is essentially a measure of visual acuity (see Materials and Methods).

Such work has shown, for example, that zooplanktivorous fishes initiate attacks on large prey from greater distances than on small prey and that darkly pigmented prey are attacked from greater distances than lightly pigmented prey [reviewed in Lazzaro, 1987; O'Brien, 1987]. More detailed behavioral studies have allowed the characterization of the search space for several species [Luecke and O'Brien, 1981; Dunbrack and Dill, 1984; Evans and O'Brien, 1988; O'Brien et al., 1989]. The ecological significance of search space geometry, and the manner in which it is

scanned, have been discussed elsewhere [O'Brien et al., 1989, 1990].

Recent work [summarized in O'Brien et al., 1990] has shown that the mean of reaction or pursuit distance measurements represents an underestimate of the fish's visual acuity. The reasons for this are as follows. Animals foraging for discrete, isolated resources have generally been characterized as using either 'ambush' or 'cruise' search strategies. Ambush foragers move infrequently and wait for a prey to enter their search space before attacking it. It is generally assumed that ambushers scan for prey only at the outer boundary of their search space. Cruise foragers move more or less continuously and, like ambushers, scan only the outer boundary of their search space for prey. An intermediate search strategy that has been observed in several species of zooplanktivorous fishes is characterized by a stop-and-go pattern of motion and has been termed *saltatory search*. Saltatory searching animals scan for prey throughout the search space, but only during brief stationary peri-

ods. If a prey is not located, they swim a short distance before stopping to scan again [O'Brien et al., 1986, 1989, 1990; Evans and O'Brien, 1988].

For both ambush and cruise searchers, most prey are located within a narrow range of distances corresponding to the limits of the search space. For these animals, average pursuit distance is a reasonable approximation of maximum pursuit distance (MxPD) and, therefore, visual acuity. However, for an animal using a saltatory search strategy, scanning nearly the entire search space while stationary, the average pursuit distance will substantially underestimate MxPD and will, therefore, underestimate visual acuity [O'Brien et al., 1990]. For the saltatory searcher, only the longest observed pursuit or reaction distances are at or near the outer boundary of the search space; therefore, the *maximum* distance to which the fish pursues (or reacts to) a prey of known size provides a more realistic measure of visual acuity than mean pursuit or reaction distance.

The resolving power of fish lenses is better than that of their retinæ [Tamura, 1957; Powers and Easter, 1983; van der Meer and Anker, 1984] and, therefore, photopic visual acuity depends primarily upon the solid angle viewed by the eye (which is related to the distance at which an object is being viewed), the spacing of cone photoreceptors across the retina and the convergence of the cones onto higher-order processing (ganglion) cells and visual centers in the brain. In general, histological measures of acuity in fishes have been obtained from counts of photoreceptor and/or ganglion cell numbers along with some estimate of the eye's focal length [Northmore and Dvorak, 1979; Breck and Gitter, 1983; Neave, 1984; Collin and Pettigrew, 1988a, b, 1989]. Such estimates are based on the assumption that (photopic) acuity is limited by the intercone spacing in the retinal mosaic (the Helmholtz postulate).

Several studies have correlated retinal structure and photoreceptor and/or ganglion cell topography with the environmental light conditions under which the species lives. For example, fishes living under low light conditions generally have retinæ organized to increase the capture of photons [Engstrom, 1963; Anctil, 1969; Ali, 1981; Ali and Klyne, 1985; Pankhurst, 1987; Henderson and Northcote, 1988]. Retinal structure has also been correlated with the direction of lens movement in fishes with different life-styles; species in which the lens moves along the eye's horizontal meridian exhibit a corresponding increase in

photoreceptor density along that axis [Tamura, 1957; Tamura and Wisby, 1963; Sivak, 1973].

Retinal topography in fishes has also been correlated with their general foraging ecology [Ahlbert, 1969, 1976; Collin and Pettigrew, 1988a, b]. For example, the retina of the rock bass (*Ambloplites rupestris*) contains a temporodorsal area of high double-cone density that correlates with the main visual direction for prey detection in this species, i.e. below the horizontal plane [Williamson and Keast, 1988].

In characterizing the search space for the zooplanktivorous white crappie (*Pomoxis annularis*), we found that the relative number of pursuits, and their maximum distances, varied across the visual field (fig. 2). We hypothesized that this variability would be reflected in a histological measure of photopic visual acuity, the density of cone photoreceptor cells. In this report we compare our behavioral measure of visual acuity, MxPD, with the topography of cone cells in the retina. The correlation between these two measures is discussed in terms of the species' foraging ecology and the 'terrain theory' of retinal topography [Hughes, 1977] which suggests that the distribution of cells across the retina is related to the symmetry or openness of the environment perceived by the animal.

## Materials and Methods

### *Experimental Organism*

The white crappie, a moderately large, deep-bodied sunfish (Centrarchidae), is an obligate zooplanktivorous predator until 15–17 cm in length [O'Brien et al., 1984]. Crappie forage in the pelagic zone of many warm-water lakes and reservoirs throughout North America [Scott and Crossman, 1973] and generally search for prey (mostly *Daphnia* sp.) at several meters depth [O'Brien et al., 1984; O'Brien and Wright, 1985].

As overseen by the NIH and NSF certified Animal Care Unit of the University of Kansas, the original research reported herein conformed to all ethical and legal guidelines governing research on vertebrate animals.

### *Behavioral Procedures*

The search behavior of juvenile white crappie was examined by observing 4 fishes (12–15 cm total length), feeding 2 at any given time, in a 90 × 90 × 90 cm aquarium filled to a depth of 30 cm. The outside of the aquarium was covered with white styrofoam to insulate it and to visually isolate the fishes from external distractions. The feeding behavior of the fish was videotaped using a JVC 100 color video camera mounted 1.5 m above the bottom of the tank. While the fishes fed, their activities were described and recorded onto the audio portion of the videotape by two observers watching through small windows located on opposite sides of the aquarium.

Lighting was provided by two rheostat-controlled 150-watt in-

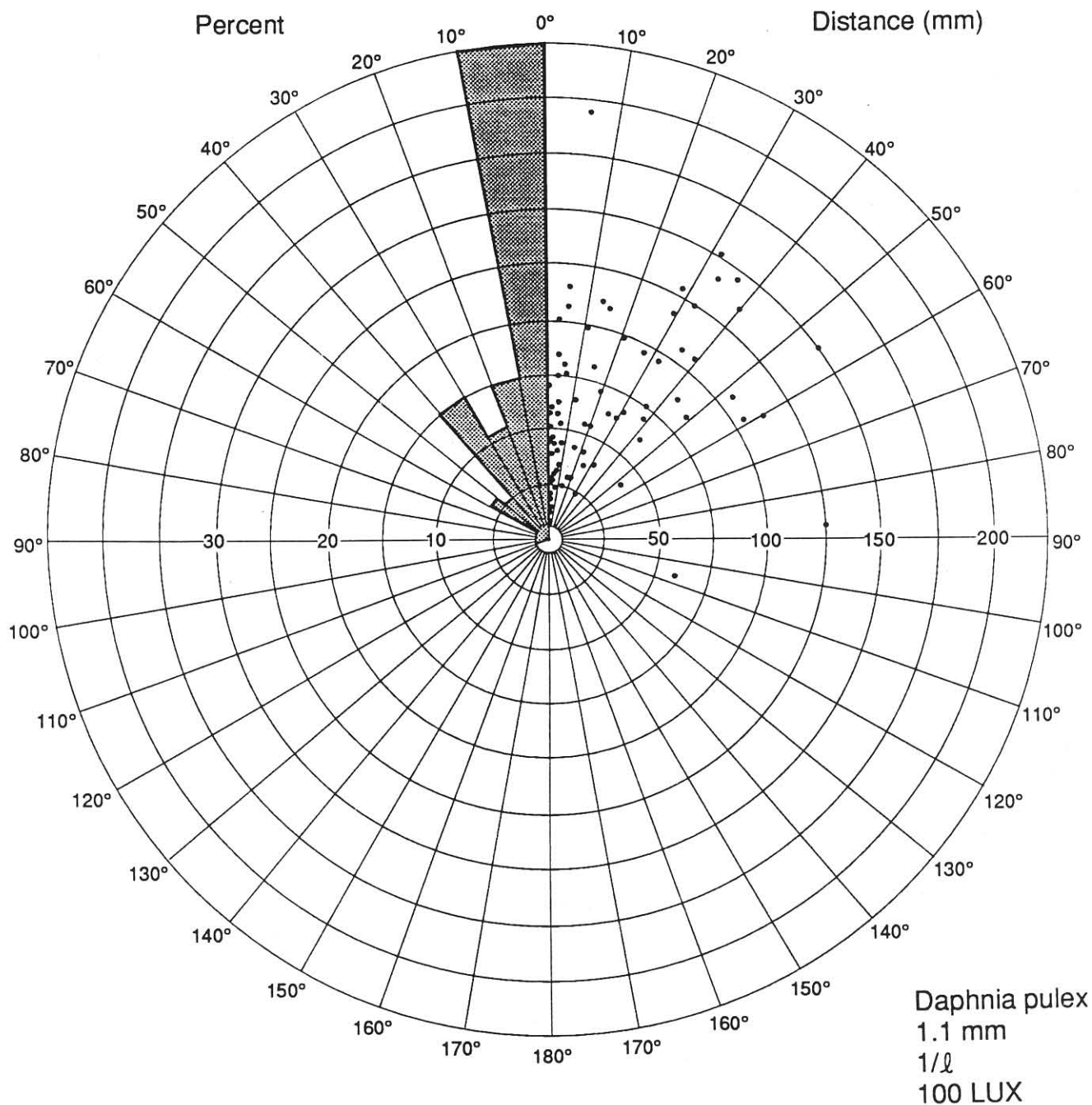




Fig. 2. Pursuit angles and distances for the white crappie (*P. annularis*) feeding on 1.1-mm *D. pulex* at a light intensity of 100 lx are plotted on the right side of this figure. Each point on the right-hand side represents a single prey location-pursuit event. The stippled area on the left half of the figure represents the relative frequency of pursuits at 10° increments across the visual field. Note that the center of the plot represents the point between the fish's eyes.

candescent flood lights diffused by a thick white cloth suspended tent-like above the aquarium with the TV camera projecting through. Light intensity was maintained at 100–300 lx, which is above the MxPD threshold for white crappie [O'Brien and Wright, 1985]. Water temperature was maintained at 20°C and all observa-

tions were made during the early afternoon. To control for hunger, the fishes were starved for at least 24 h prior to an experiment. Separate experiments were performed using two size classes of cultured *Daphnia pulex* (mean total lengths of 1.1 and 2.0 mm) added at 1 prey/liter to the observation aquarium.

 = 1.1 mm *D. pulex*  
 = 2.0 mm *D. pulex*

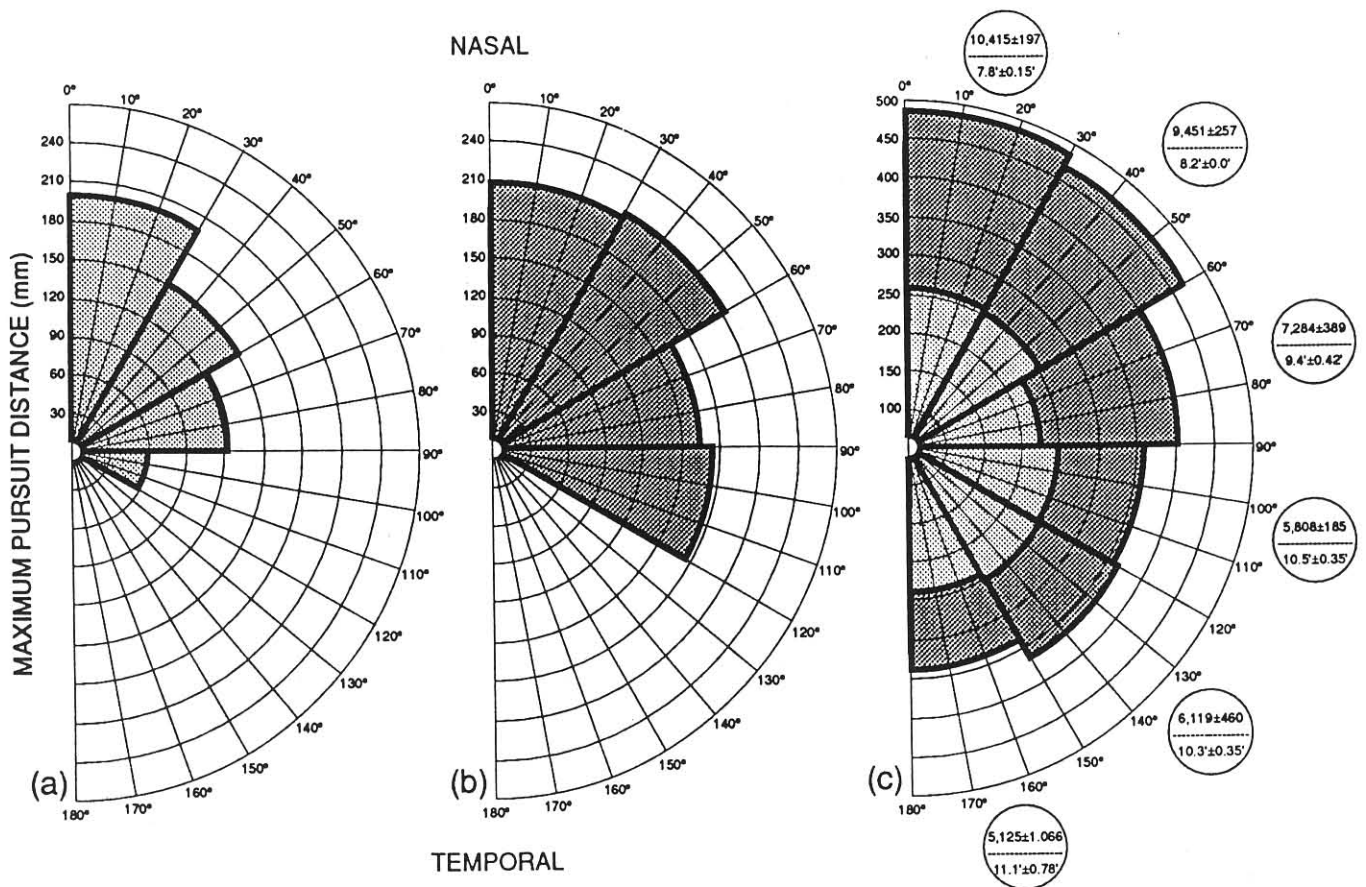


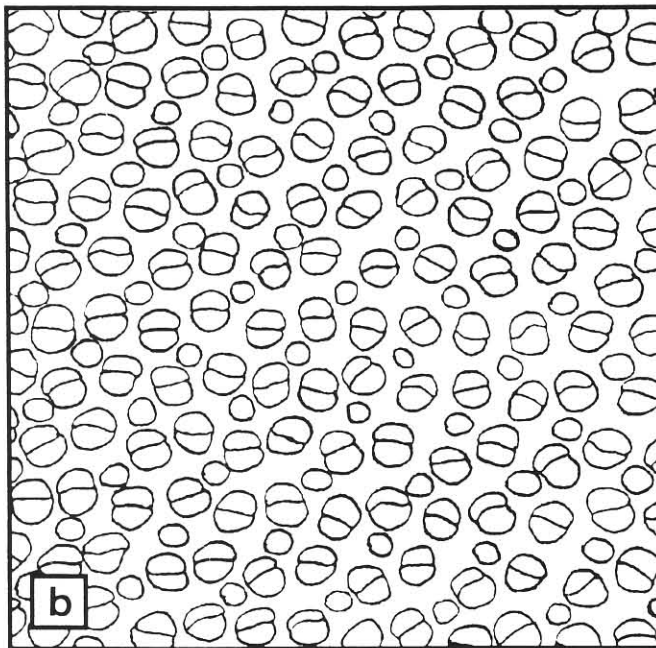
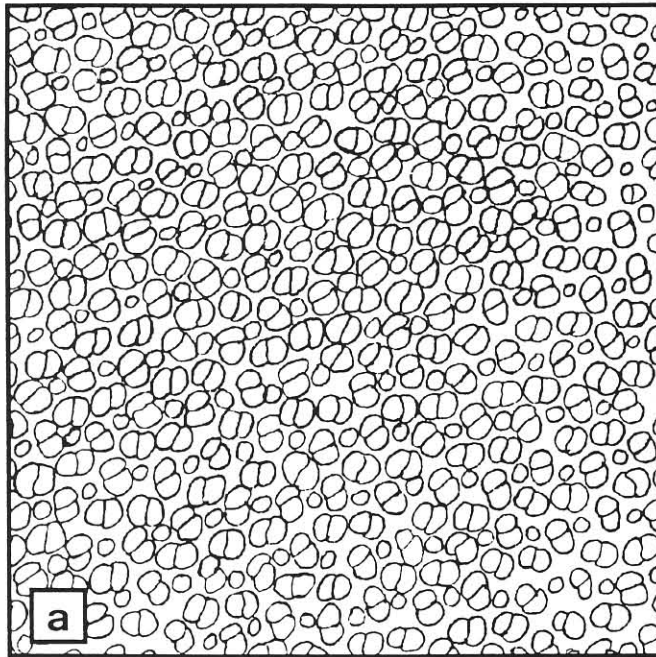
Fig. 3. MxPDs across the visual field for the white crappie (*P. annularis*) feeding on 1.1-mm *D. pulex* (a), 2.0-mm *D. pulex* (b) and calculated from cone cell topography (c). Numbers in the circles next to each 30° angle-increment in c are the cone cell densities (number per square millimeter ± their SD) in the corresponding area of the retina and the angular acuities (minutes of arc ± their SD) calculated from them.

White crappie are saltatory searchers and, as described above, they move in a stop-and-go pattern while feeding, swimming short distances and then stopping for a brief period of time before moving on. Search for prey occurs only during the stationary pauses between repositioning movements [O'Brien et al., 1986, 1989]. We define a repositioning movement that is followed by an attack on prey as a *pursuit*, while one that is not followed by an attack is termed a *run*. The videotapes were analyzed by assigning the activities of the fishes to one of the components of the feeding cycle: search, run, pursuit or attack.

Prey pursuit angles and distances, run lengths and turn angles, were marked on the television screen with a grease pencil and measured. Distances were converted to centimeters by using the ratio of the fish's actual length to its length on the television screen. It should be noted that, since vertical movements were not estimated, our distance measurements may represent slight underestimates.

The longitudinal body axis of the fish was defined as the central axis of the forward-directed visual field (fig. 1). When a prey was encountered, the pursuit angle was estimated as the angle between the central axis of the fish, prior to pursuit, and the line connecting the fish's nose to the position of the prey (determined *a posteriori* as the point at which the fish attacked the prey).

Although pursuit distances at any given angle vary [O'Brien et al., 1986; Evans and O'Brien, 1988] (fig. 2), as outlined above, only MxPDs, not mean pursuit distances, yield an accurate measure of visual acuity for saltatory searching animals. Measurements of MxPDs on prey of known size can be expressed as an angle subtended on the retina because the image of a prey item is formed by straight lines from the ends of its longest visible dimension to a point on the fish's retina. For a prey item of known size at a given distance from the eye, this visual angle ( $\alpha$ , in degrees) is calculated as:



20  $\mu$ m

**Fig. 4.** Camera lucida drawings illustrating the cone cell mosaic found in the retina of a white crappie (*P. annularis*) and the variability in intercone spacing (packing density) observed in different areas of the retina. **a** Cone packing (10,402 cones/mm<sup>2</sup>) in the temporal retina. **b** Cone packing (4,740 cones/mm<sup>2</sup>) in the nasal retina.

$$\alpha = 2 \arctan (0.5 H / MxPD), \quad (1)$$

where H is the visible size of the prey and MxPD is the maximum pursuit distance observed for any given pursuit angle [Breck and Gitter, 1983]. Thus, a 1.0-min change in visual angle corresponds to a 30-mm change in the calculated MxPD for 1.1-mm *D. pulex* and to a 55-mm change for 2.0-mm *D. pulex*.

*Daphnia* have conspicuous alga-filled guts and dark eye pigmentation. They are an example of a prey item for which core body length (the length of the gut), as opposed to total length, is the critical dimension used by the fishes in their location [Wright and O'Brien, 1982; O'Brien, 1987]. As a result, the *D. pulex* size measurements used in the calculations were total lengths multiplied by 0.55, the ratio of core to total body length for this species.

#### Histological Procedures

Four light-adapted white crappie were sacrificed by spinal section and the eyes immediately enucleated. Because cone packing changes with fish size [Hairston et al., 1982; Fernald, 1985], all of the specimens we examined (for both behavioral and histological estimates) were of approximately the same total length (151.3  $\pm$  8.9 mm). The cornea, iris, lens and as much of the vitreal fluid as possible were removed (the latter with absorbent tissue) to improve penetration of the primary fixative. Eye and lens diameters for the specimens, measured with calipers, were 12.0  $\pm$  0.07 and 4.4  $\pm$  0.05 mm, respectively. Eyecups were immersed in primary fixative (2.5% glutaraldehyde, 1% paraformaldehyde, 3% sucrose, in 0.06 M phosphate buffer) where they remained, refrigerated, for 6–12 h.

Ten to twelve disks (3 mm in diameter) of retinal tissue were removed from each eyecup using a surgical trephine. The exact positions of these disks were recorded on maps of each eye. The eyecups themselves were stored in primary fixative for future reference. The orientation of each disk was marked by cutting off the dorsal edge. Disks were placed in separate vials with primary fixative and subsequently washed in buffer (0.06 M phosphate buffer, 3% sucrose, pH 7.3), postfixed in 1% OsO<sub>4</sub>, rinsed, dehydrated in a graded ethanol series, infiltrated and embedded in Polybed 812 following the methodology of Ali and Ancia [1976].

The disks were tangentially sectioned, to the base of the cone outer segments, using a Sorvall MT 5000 ultramicrotome. Sections (1  $\mu$ m thick) were stained with toluidine blue (in boric acid) for light-microscopic examination. Camera lucida drawings (cross-sectional) of photoreceptor outer segments in sections of these oriented disks were made using a Zeiss compound microscope. Only cross-sectional outer segments, indicative of proper orientation, were traced. The numbers of double and single cones were counted by placing a 1-cm<sup>2</sup> grid over the drawings. These numbers were converted to numbers per square millimeter of retina by correcting for the magnification factor of the camera lucida system. A minimum 0.03 mm<sup>2</sup> of retina was examined for each section to estimate cone density.

Assuming that acuity is limited by the number of cones in the retina, a histological measure of acuity (minimum separable angle or angular acuity) can be calculated by dividing the linear distance between the centers of adjacent cones (the reciprocal of the number of cones per millimeter) by the focal length of the lens [Neave, 1984; Williamson and Keast, 1988]. The focal length of the lens is calculated by multiplying its radius (r) by 2.36, Matthiessen's ratio for

fish [Breck and Gitter, 1983; Fernald, 1988]. This yields the following expression:

$$\sin \alpha = 1.11/(\sqrt{N} \times 2.36r), \quad (2)$$

where  $\alpha$  is the angular acuity (minimum separable angle) in degrees, 1.11 represents an 11% correction factor to account for histological shrinkage of the retina prior to cone density measurements, and  $N$  is the number of cone cells (doubles and singles) per square millimeter [Neave, 1984]. This equation assumes that in order for two objects to be differentiated their images must be separated by at least 1 photoreceptor. Note that a 1.0-min change in angular acuity corresponds to a difference of approximately 2,500 cones/mm<sup>2</sup> on the retina.

#### Comparison of Behavioral and Histological Data

Since white crappie scan a wedge-shaped search space of limited height (a maximum of approximately 10 cm above the eye's horizontal meridian; fig. 1), represented by a narrow nasal-temporal band on the retina, comparison of the two measures of acuity was limited to this area and was accomplished as follows.

We observed that when white crappie scan for prey their eyes are oriented perpendicular to the antero-posterior axis of the body (i.e. 90° from forward-directed). It is only after locating a prey item that the eyes rotate nasally, an action most likely to increase the binocular field and thereby improve depth perception. It is reasonable to assume that a line extending back to the retina along the angle at which a prey item is pursued represents the point at which the image is first formed on the retina. Thus, the MxPD in this area of the visual field can be compared to the density of cone cells in the corresponding area of the retina.

Mean cone cell densities in 6 areas of the retina, spaced at equal distances along a line approximately 5 cm thick running along a nasal-temporal band just below the horizontal meridian (corresponding to the behaviorally determined projection of the visual field), were compiled from counts of all 8 eyes. Cone cell densities were converted to angular acuities using equation 2. The MxPDs expected from these angular acuities were then calculated by solving for MxPD in equation 1. These calculations were made for both *D. pulex* size classes used in the behavioral experiments.

The MxPDs obtained in the experiments on the two size classes of *D. pulex* were compiled, at 30° increments (representing the 6 retinal areas for which angular-acuity calculations were made), from 0° forward-directed to 180° from forward-directed.

## Results

### Behavioral Acuity

Right and left pursuit angles and distances, which were mirror images, were combined and are presented in the right visual field (fig. 2, 3). The greatest number of pursuits occurs in the 0–30° wedge of the visual field; 87% of all pursuits also occur in this area (fig. 2, 3a, b). As expected, MxPDs are generally longer for 2.0-mm *D. pulex*. Observed MxPDs generally decrease as pursuit angles increase from 0 to

180° from forward-directed for both size classes (fig. 3a, b). Very few pursuits are observed at angles greater than 60° from forward-directed (fig. 2). It should also be pointed out that, for a wedge-shaped search space, the volume of water searched decreases nonlinearly as MxPD decreases.

### Histological Acuity

The photoreceptor cell layer of the retina in the white crappie is similar to that described in the black crappie, *Pomoxis nigromaculatus* [Ali and Ancil, 1976, p. 171, plate 81.4], and in other zooplanktivorous teleosts [e.g. Engstrom, 1963; Ahlbert, 1969, 1976]. A single central cone is surrounded by four equal double cones in a square mosaic pattern, and differences in cone packing densities across the retina are clear (fig. 4). There are no gross changes in the mosaic pattern across the retina, although the orientation of double-cone axes in alternating rows does alter slightly from the perpendicular orientation of a typical square mosaic. This modified square mosaic has been described for the largemouth bass, *Micropterus salmoides* [Eigenmann and Shafer, 1900], and has also been observed in several other species [Lyll, 1957; Engstrom, 1963; Ahlbert, 1969, 1976]. We have observed a small number (5–10/0.01 mm<sup>2</sup>) of triple cones interspersed among single and equal doubles in a restricted area of the temporoventral retina approximately 20° from the vertical meridian. Triple cones interspersed with doubles and singles have been reported in the retina of the brown trout (*Salmo trutta*) [Lyll, 1957].

In general, the number of cone cells, and therefore angular acuity, is highest in a restricted area of the far temporal retina along the horizontal meridian (fig. 5a). Cone cell densities in the corresponding region of the nasal retina are approximately half these values (fig. 5b). The number of cones generally decreases dorsally and ventrally of the horizontal meridian (fig. 5a, b). Exceptions to this trend are noted in the nasal retina in which cone cell numbers increase approximately halfway between the horizontal and vertical meridians, both dorsally and ventrally (fig. 5b).

### Comparison of Behavioral and Histological Acuities

The MxPDs calculated from cone cell densities across the nasal-to-temporal visual field were compared against those observed in the behavioral experiments on polar coordinate plots. The MxPDs calcu-

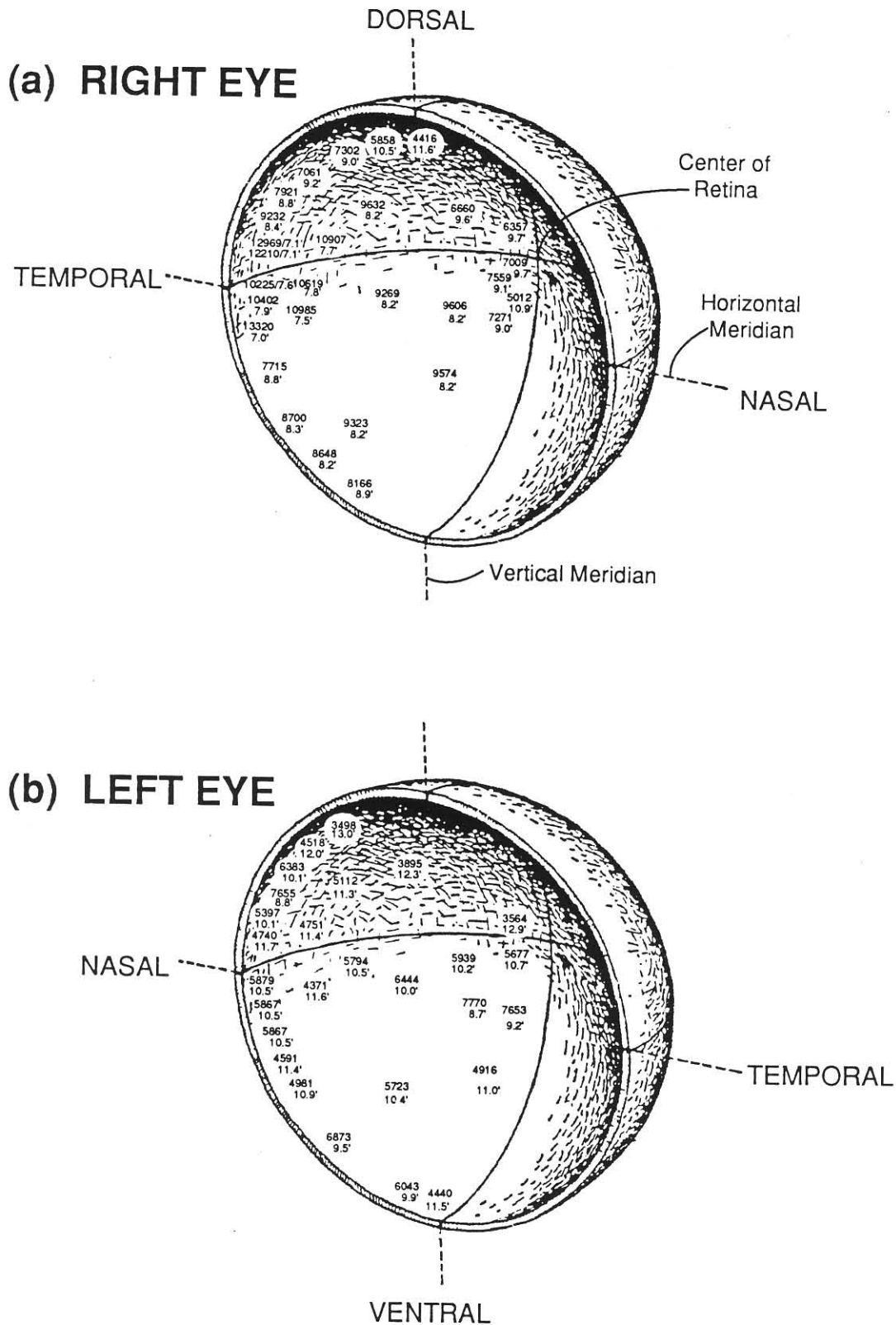


Fig. 5. Topographic maps of cone cell numbers and minimum separable angles (in minutes of arc) calculated from them in the retinae of white crappie (*P. annularis*). To maintain a three-dimensional effect, numbers for the temporal retina were plotted on a composite map of the right eye (a) and those for the nasal area were plotted on a map of the left eye (b).



lated from the histological measure of acuity are greatest in the 0–30° wedge of the visual field and generally decrease to 180° from forward-directed (fig. 3c). The same trend is observed in the behavioral data, although the absolute values for MxPD calculated from cone cell density are 2–3 times those observed (fig. 3). The ratio of histologically calculated MxPDS to observed MxPDs is not consistent across the visual field but increases with the angle from forward-directed.

## Discussion

### *Behavioral Acuity*

In the white crappie, the greatest number of pursuits, and those of greatest distance, occur in the 0–30° wedge of the visual field (fig. 2, 3). Similar patterns of prey pursuit angles and distances have been observed in other saltatory searching zooplanktivores. Prey location ability in the bluegill sunfish (*Lepomis macrochirus*) is greatest in the forward-directed hemisphere, and both the probability of pursuing a prey and the pursuit length decline steadily caudally, dorsally and ventrally [Luecke and O'Brien, 1981]. In the Arctic grayling (*Thymallus arcticus*), most pursuits occur in the first 50° of the visual field [Evans and O'Brien, 1988], and in coho salmon (*Oncorhynchus kisutch*) most pursuits are in the dorsal, forward-directed area [Dunbrack and Dill, 1984].

### *Correlation between Foraging Behavior and Cone Cell Topography*

The maximum density of cones in the white crappie occurs in the temporal retina near the horizontal meridian. Cone densities decrease nasally, dorsally and ventrally. Qualitatively, this distribution is consistent with the pattern of foraging behavior exhibited by white crappie: they scan a wedge-shaped search space of limited height and angle (fig. 1, 2). Quantitatively, the distribution of MxPDs in the horizontal visual field, as calculated from cone densities, is consistent with the trend in MxPDs observed behaviorally (fig. 3). It is worth noting that white crappie are better able to discriminate the absolute size of prey when the prey is located in the forward-directed visual field [O'Brien et al., 1985].

Similar correlations between retinal topography and foraging behavior have been reported in other fishes. As mentioned above, the main visual direction for prey detection in the rock bass is below the hori-

zontal plane, which correlates with a temporodorsal area of high double-cone density in the retina [Williamson and Keast, 1988]. In the common pope or ruffe (*Acerina cernua*), a bottom-dwelling benthivore, the highest cone density is in the nasal region, perhaps for predator detection [Ahlbert, 1969]. In the white crappie, the number of cones increases halfway between the horizontal and vertical meridians in the dorsal and ventronasal retina (fig. 5b). We suggest that this would increase the white crappie's response distance to potential predators, which may approach from above, below or behind.

Increased cone densities toward the retinal periphery, particularly in the temporal area, have been reported in other zooplanktivorous fishes, for example the seven species of haplochromine cichlids examined by van der Meer and Anker [1984]. O'Connell [1963] suggested that 'the ability to resolve smaller objects near or far in the forward part of the field would require a refined cone screen in the temporal part of the retina' (p. 315), a pattern that he observed in six species of pelagic marine teleosts. A marked increase in the horizontal temporal retina, with the lowest density in the dorsal and ventral nasal areas, has been reported in the yellow perch (*Perca fluviatilis*) [Ahlbert, 1969], and a region of high cone density has been observed in the ventrotemporal part of the retina in Atlantic salmon (*Salmo salar*), brown trout [Ahlbert, 1976] and in several other species [reviewed by Ahlbert, 1976].

The maximum acuities calculated from cone cell density in the white-crappie retina were 7.0 min; similar values have been reported for other teleosts [reviewed by Blaxter, 1970; Powers and Easter, 1983].

### *Comparison of Behavioral and Histological Measures of Acuity*

Although the trends in white-crappie MxPDs determined behaviorally and histologically are consistent, the behavioral estimates are shorter (fig. 3). Such overestimates in histologically determined acuities have been reported in several other studies [reviewed by Powers and Easter, 1983, p. 384]. For example, minimum separable angles for the skipjack tuna (*Katsuwonus pelamis*), determined histologically from cone counts [Tamura and Wisby, 1963], are smaller than those determined behaviorally from the fish's ability to discriminate between horizontally and vertically striped images [Nakamura, 1968]. Further, Yamanouchi's [1956] data for visual acuity in the con-

vict fish (*Microcanthus strigatus*) was reworked into visual-acuity estimates by Nakamura [1968] who concluded that the behavioral estimate of acuity (4.98 min) was poorer than that determined from cone cell density (3.60 min). Visual acuity in the bluegill sunfish has been estimated at 2.7 min [Williamson and Keast, 1988], from which an MxPD of 77 cm (for a 1.1-mm *D. pulex*) can be calculated. This value is several times greater than the largest reaction distances observed for this species [Vinyard and O'Brien, 1976; Luecke and O'Brien, 1981].

As already noted, visual acuity is dependent not only upon the intercone spacing but also upon the degree of convergence between cone cells and nerve cells at higher processing levels. It is likely that estimates of visual acuity based upon intercone spacing are higher than those observed behaviorally, because counts of cone cell density alone do not take signal convergence and processing into account. The support for this statement is as follows.

It has been proposed that the four equal double cones and central single cone of a square mosaic represent a functional visual unit [Wagner, 1978; van der Meer and Anker, 1984]. Several lines of evidence support this hypothesis. Firstly, cone convergence ratios of 5:1 (cones: ganglion cells) have been reported in seven species of haplochromine cichlids with square mosaic retinæ [van der Meer and Anker, 1984]. Further, electrophysiological estimates of the minimum resolvable angle in goldfish retinal ganglion cells [Schwassmann, 1975], where convergence has been taken into account, are much closer to behavioral estimates of visual acuity in this species [Powers and Easter, 1983]. Finally, the diameter of retinal ganglion cell receptive-field centers in goldfish can exceed  $10^\circ$  [Beauchamp and Daw, 1972; Macy and Easter, 1981]; this is about the angle that would be subtended on the retina by the two size classes of *D. pulex* at the MxPDs observed in the  $0\text{--}30^\circ$  wedge of the visual field. It should also be noted that substantially higher cone:ganglion cell convergence ratios have been reported in other species with square mosaics, for example 13:1 for the bluegill sunfish [Williamson and Keast, 1988]. However, convergence ratios across the retina are heterogeneous, often approaching 1:1 in areas of high photoreceptor cell concentration while being considerably higher (e.g. 40:1) in areas of low photoreceptor cell abundance [Wagner, 1978; Williamson and Keast, 1988]. Increased convergence ratios toward the nasal retina in the white crappie

are a possible explanation why MxPDs observed behaviorally fall off more drastically with increasing angle off forward-directed than would be predicted from cone cell numbers alone (fig. 3).

#### *Cone Mosaic and Visual Acuity*

Cone photoreceptors in many teleost retinæ are arranged in mosaic patterns, the most common of which are the row and square mosaics [Eigenmann and Shafer, 1900; Lyall, 1957; Engstrom, 1963; Ancil, 1969; Wagner, 1978]. In both of these patterns, a row of equal (or unequal) double cones alternates with a row of single cones; rods are always interspersed among the cone array, sometimes in a regular pattern of their own [Wagner, 1978]. In a square mosaic, the double cones (each one of which may contain the same or different photopigments [Fernald, 1988]) are arranged so that the plasma membranes at the contact zone between each photoreceptor outer segment, which appears on a micrograph as a line through the center of each pair, are at right angles to one another. In a row mosaic the axes of the double cones are parallel to one another. In some species, both patterns exist in different regions of adult retinæ or occur at different times during development [e.g. Ahlbert, 1969, 1976].

These mosaic patterns are not limited to the photoreceptor layer but are carried into the external plexiform layer at the level of the cone pedicles: the processes of cone horizontal cells reflect the mosaic of the photoreceptors that they contact [Wagner, 1978]. Several double cones diverge onto different cone horizontal cells, and this divergence may contribute to the anatomical basis for a high degree of lateral inhibition in the processing of visual information in mosaic retinæ [Wagner, 1978]. This extensive system of lateral inhibition may be associated with the visual contrast (border) enhancement observed in the bluegill sunfish, another centrarchid that possesses a square mosaic [Williamson and Keast, 1988]. These fishes can detect prey items that are less than 1% brighter than the visual background [Hawryshyn et al., 1988].

Based upon correlations between the presence of a square mosaic and a life-style dependent upon motion detection, regular cone mosaics are generally considered to represent an adaptational advantage for the discrimination of movement [Lyall, 1957; Engstrom, 1963; Ancil, 1969; Ahlbert, 1976; Fernald, 1988]. The physiological basis for this improved mo-

tion detection apparently lies in the high degree of lateral inhibition in mosaic retinæ which results in enhanced directional sensitivity [Wagner, 1978, p. 47]. It is thought that row mosaics favor the perception of movements in two directions and square mosaics movements in all directions [Bathelt, 1970; Wagner, 1978], although this has not been rigorously tested. Reaction distances in zooplanktivorous fishes with square mosaic retinæ, including the white crappie, are much greater for moving than for stationary prey [Wright and O'Brien, 1982; reviewed by Lazzaro, 1987].

#### *Terrain Theory and Retinal Topography in the White Crappie*

The terrain theory [Hughes, 1977] suggests that the topography of cells across the retina is related to the symmetry of the perceived world. In species whose visual environment is unobscured, an increase in photoreceptor and/or ganglion cell density across the horizontal meridian is observed. This retinal streak allows an animal to scan a broad horizon, without the distinctive eye movements that would be necessary for scanning with an area centralis, and to perceive movement at a lower threshold [see Collin and Pettigrew, 1988b].

Horizontal band-shaped retinal areas have been found in several teleosts, usually open-water species, which also exhibit a relative increase in the size of the optic tectum [reviewed by Collin and Pettigrew, 1988b]. The retina in the white crappie possesses a temporal area of increased cone density and a horizontal streak (fig. 5). As previously noted, this species is an open-water fish that searches for prey in an environment with little or no structure, and the topography of cone cells in its retina is, therefore, consistent with the terrain theory. As juveniles, white crappie are open-water zooplanktivores, while as larvae and adults they are littoral-zone (with far more visible structure) foragers. It would be of interest to examine individuals from these age classes to see if retinal topography changes in accordance with the terrain theory.

To summarize, we have used our observations of maximal prey pursuit distances in a zooplanktivorous fish as a behavioral estimate of visual acuity. The MxPDs are greatest in the first 30° of the visual field and decrease as the angle from forward-directed increases. The same trend is observed in a histological measure of visual acuity, the number of cone cells per

unit area in the retina. Differences in absolute values of minimum separable angle calculated from the two measures (histological estimates of acuity are higher) are likely to be the result of cone cell counts alone not accounting for higher-order processing in the visual system. We conclude that the behavioral measure represents a more realistic estimate of visual acuity in this animal.

#### Acknowledgments

This work was supported by NSF grant BSR-8717454 and a University of Kansas Biomedical Research Fund Grant to W.J.O'B. H.I.B. was supported by a postgraduate scholarship from the Natural Sciences and Engineering Research Council of Canada (NSERC), by a bursary from the Quebec Ministry of Higher Education and Science and, during manuscript preparation, by an E.B. Eastburn postdoctoral fellowship from the Hamilton Foundation of Canada. B.I.E. was supported by a postdoctoral fellowship from NSERC Canada. The Sorvall MT-5000 ultramicrotome was purchased with funds made available by the J.R. and Inez W. Jay Research Fund of the University of Kansas Endowment Association, allocation No. 5058-X705 to W.C.G. We thank Isabelle Bernard for helping to analyze the data. Nancy Dahl, Craig Hawryshyn, Henny van der Meer and an anonymous reviewer provided comments that improved the manuscript.

#### References

- Ahlbert, I.B. (1969) The organization of the cone cells in the retinæ of four teleosts with different feeding habits (*Perca fluviatilis* L., *Lucioperca lucioperca* L., *Acerina cernua* L. and *Coregonus albula* L.). *Ark. Zool. Ser.* 2, 22: 445-481.
- Ahlbert, I.B. (1976) Organization of the cone cells in the retinæ of salmon, *Salmo salar* and trout, *Salmo trutta trutta*, in relation to their feeding habits. *Acta Zool.*, 57: 13-35.
- Ali, M.A. (1981) Adaptations rétinienne aux habitats. *Rev. Can. Biol.*, 40: 3-17.
- Ali, M.A., and M. Anctil (1976) *The Retinas of Fishes: An Atlas*. Springer, Berlin.
- Ali, M.A., and M.A. Klyne (1985) Phylogeny and functional morphology of the vertebrate retina. *Fortschr. Zool.*, 30: 634-648.
- Anctil, M. (1969) Structure de la rétine chez quelques téléostéens marins du plateau continental. *J. Fish. Res. Board Can.*, 26: 597-628.
- Bathelt, D. (1970) Experimentelle und vergleichende morphologische Untersuchungen am visuellen System von Teleostiern. *Zool. Jahrb. Abt. Anat. Ontog.*, 87: 402-470.
- Beauchamp, R.D., and N.W. Daw (1972) Rod and cone input to single goldfish optic nerve fibers. *Vision Res.*, 12: 1201-1212.
- Blaxter, J.H.S. (1970) Light. Animals. Fishes. *In Marine Ecology*, Vol. I. Environmental Factors, Part 1 (ed. by O. Kinne), Wiley-Interscience, New York, pp. 213-320.
- Breck, J.E., and M.J. Gitter (1983) Effect of fish size on the reactive

- distance of bluegill (*Lepomis macrochirus*) sunfish. *Can. J. Fish. Aquat. Sci.*, *40*: 162-167.
- Collin, S.P., and J.D. Pettigrew (1988a) Retinal topography in reef teleosts. I. Some species with well-developed areas but poorly developed streaks. *Brain, Behav. Evol.*, *31*: 269-282.
- Collin, S.P., and J.D. Pettigrew (1988b) Retinal topography in reef teleosts. II. Some species with prominent horizontal streaks and high-density areas. *Brain, Behav. Evol.*, *31*: 283-295.
- Collin, S.P., and J.D. Pettigrew (1989) Quantitative comparison of the limits on visual spatial resolution set by the ganglion cell layer in twelve species of reef teleosts. *Brain, Behav. Evol.*, *34*: 184-192.
- Douglas, R.H., and M.B.A. Djamgoz (1990) *The Visual System of Fish*. Chapman & Hall, London.
- Dunbrack, R.L., and L.M. Dill (1984) Three dimensional prey reaction field of the juvenile coho salmon (*Oncorhynchus kisutch*). *Can. J. Fish. Aquat. Sci.*, *41*: 1176-1182.
- Eigenmann, C.H., and G.D. Shafer (1900) The mosaic of single and twin cones in the retina of fishes. *Am. Nat.*, *34*: 109-118.
- Engstrom, K. (1963) Cone types and cone arrangements in teleost retinæ. *Acta Zool.*, *44*: 179-243.
- Evans, B.I., and W.J. O'Brien (1988) A reevaluation of the search cycle of planktivorous Arctic grayling, *Thymallus arcticus*. *Can. J. Fish. Aquat. Sci.*, *45*: 187-192.
- Fernald, R.D. (1985) Growth of the teleost eye: novel solution to complex constraints. *Env. Biol. Fishes*, *13*: 113-123.
- Fernald, R.D. (1988) Aquatic adaptations in fish eyes. *In* *Sensory Biology of Aquatic Animals* (ed. by J. Atema, R.R. Fay, A.N. Popper, et al.), Springer, New York, pp. 435-466.
- Fernald, R.D. (1989) Teleost vision. *In* *Development of the Vertebrate Retina* (ed. by B.L. Finlay and D.R. Sengelaub), Plenum Press, New York, pp. 247-265.
- Guthrie, D.M. (1983) Integration and control by the central nervous system. *In* *Control Processes in Fish Physiology* (ed. by J.C. Rankin, T.J. Pitcher and R.T. Duggan), Wiley, New York, pp. 130-154.
- Hairston, N.G., Jr., K.T. Li, and S.S. Easter, Jr. (1982) Fish vision and the detection of planktonic prey. *Science*, *218*: 1240-1242.
- Hawryshyn, C.W., M.G. Arnold, W.N. McFarland, and E.R. Loew (1988) Aspects of color vision in bluegill sunfish (*Lepomis macrochirus*): ecological and evolutionary relevance. *J. Comp. Physiol. A*, *164*: 107-116.
- Henderson, M.A., and T.G. Northcote (1988) Retinal structure of sympatric and allopatric populations of cutthroat trout (*Salmo clarki clarki*) and dolly varden char (*Salvelinus malma*) in relation to their spatial distribution. *Can. J. Fish. Aquat. Sci.*, *45*: 1321-1326.
- Herter, K. (1953) *Die Fischdressuren und ihre sinnesphysiologischen Grundlagen*. Akademie, Berlin.
- Hughes, A. (1977) The topography of vision in mammals of contrasting life style: comparative optics and retinal organisation. *In* *The Visual System in Vertebrates* (ed. by F. Crescitelli), *Handbook of Sensory Physiology*, Vol. VII/5, Springer, Berlin, pp. 613-756.
- Lazzaro, X. (1987) A review of planktivorous fishes: their evolution, feeding behaviours, selectivities, and impacts. *Hydrobiologia*, *146*: 97-167.
- Luecke, C., and W.J. O'Brien (1981) Prey location volume of a planktivorous fish: a new measure of prey vulnerability. *Can. J. Fish. Aquat. Sci.*, *38*: 1264-1270.
- Lyall, A.H. (1957) Cone arrangements in teleost retinæ. *Q. J. Microscop. Sci.*, *98*: 189-201.
- Macy, A., and S.S. Easter, Jr. (1981) Growth-related changes in the size of receptive field centers of retinal ganglion cells in goldfish. *Vision Res.*, *21*: 1497-1504.
- Meer van der H.J., and G.Ch. Anker (1984) Retinal resolving power and sensitivity of the photopic system in seven haplochromine species (Teleostei, Cichlidae). *Neth. J. Zool.*, *34*: 197-209.
- Nakamura, E.L. (1968) Visual acuity of two tunas, *Katsuwonus pelamis* and *Euthynnus affinis*. *Copeia*, *1968*: 41-49.
- Neave, D.A. (1984) The development of visual acuity in larval plaice (*Pleuronectes platessa* L.) and turbot (*Scophthalmus maximus* L.). *J. Exp. Mar. Biol. Ecol.*, *78*: 176-175.
- Northmore, D.P.M., and C.A. Dvorak (1979) Contrast sensitivity and acuity of the goldfish. *Vision Res.*, *19*: 255-261.
- O'Brien, W.J. (1979) The predator-prey interactions of planktivorous fish and zooplankton. *Am. Scientist*, *67*: 572-581.
- O'Brien, W.J. (1987) Planktivory by freshwater fish: thrust and parry in the pelagia. *In* *Predation: Direct and Indirect Impacts on Aquatic Communities* (ed. by W.C. Kerfoot and A. Sih), University Press of New England, Hanover, pp. 3-16.
- O'Brien, W.J., and D.I. Wright (1985) Potential limits on the daytime planktivorous feeding depth of white crappie. *Verh. Int. Verein. Limnol.*, *22*: 2527-2533.
- O'Brien, W.J., B. Loveless, and D. Wright (1984) Feeding ecology of young white crappie in a Kansas reservoir. *North Am. J. Fish. Manag.*, *4*: 341-349.
- O'Brien, W.J., B. Evans, and C. Luecke (1985) Apparent size choice of zooplankton by planktivorous sunfish: exceptions to the rule. *Env. Biol. Fishes*, *13*: 225-233.
- O'Brien, W.J., B.I. Evans, and G.L. Howick (1986) A new view of the predation cycle of a planktivorous fish, white crappie (*Pomoxis annularis*). *Can. J. Fish. Aquat. Sci.*, *43*: 1894-1899.
- O'Brien, W.J., B.I. Evans, and H.I. Browman (1989) Flexible search tactics and efficient foraging in saltatory searching animals. *Oecologia*, *80*: 100-110.
- O'Brien, W.J., H.I. Browman, and B.I. Evans (1990) The search behavior of foraging animals. *Am. Scientist*, in press.
- O'Connell, C.P. (1963) The structure of the eye of *Sardinops caerulea*, *Engraulis mordax*, and four other pelagic marine teleosts. *J. Morphol.*, *113*: 287-330.
- Pankhurst, N.W. (1987) Intra- and interspecific changes in retinal morphology among mesopelagic and demersal teleosts from the slope waters of New Zealand. *Env. Biol. Fishes*, *19*: 269-280.
- Powers, M.K., and S.S. Easter, Jr. (1983) Behavioral significance of retinal structure and function in fishes. *In* *Fish Neurobiology*, Vol. 1. *Brain Stem and Sense Organs* (ed. by R.G. Northcutt and R.E. Davis), University of Michigan Press, Ann Arbor, pp. 377-404.
- Schwassmann, H.O. (1975) Refractive state, accommodation, and resolving power of the fish eye. *In* *Vision in Fishes: New Approaches to Research* (ed. by M.A. Ali), Plenum Press, New York, pp. 279-287.
- Scott, W.B., and E.J. Crossman (1973) *Freshwater Fishes of Canada*. Fisheries Research Board of Canada, Ottawa, Bull. No. 184.
- Sivak, J.G. (1973) Interrelation of feeding behavior and accommodative lens movements in some species of North American freshwater fishes. *J. Fish. Res. Board Can.*, *30*: 1141-1146.

- Tamura, T. (1957) A study of visual perception in fish, especially on resolving power and accommodation. *Bull. Jap. Soc. Sci. Fish.*, 22: 536-557.
- Tamura, T., and W.J. Wisby (1963) The visual sense of pelagic fishes, especially the visual axis and accommodation. *Bull. Mar. Sci. Gulf Caribbean*, 13: 433-448.
- Vinyard, G.L., and W.J. O'Brien (1976) Effects of light and turbidity on the reactive distance of bluegill (*Lepomis macrochirus*). *J. Fish. Res. Board Can.*, 33: 2845-2849.
- Wagner, H.-J. (1978) Cell types and connectivity patterns in mosaic retinas. *Adv. Anat. Embryol. Cell Biol.*, 55: 1-81.
- Williamson, M., and A. Keast (1988) Retinal structure relative to feeding in the rock bass (*Ambloplites rupestris*) and bluegill (*Lepomis macrochirus*). *Can. J. Zool.*, 66: 2840-2846.
- Wright, D.I., and W.J. O'Brien (1982) Differential location of *Chaoborous* larvae and *Daphnia* by fish: the importance of motion and visible size. *Am. Midl. Natural.*, 108: 68-73.
- Yamanouchi, T. (1956) The visual acuity of the coral fish *Microcanthus strigatus* (Cuvier and Valenciennes). *Publ. Secto Mar. Biol. Lab.*, 5: 133-156.

Howard I. Browman, PhD  
Département des sciences biologiques  
Université de Montréal  
CP 6128, succursale A  
Montréal, Qué. H3C 3J7 (Canada)