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Coherence in nervous system design: the visual system of *Pantodon buchholzi*

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One of the more unusual visual systems of the Actinopterygii is that of *Pantodon buchholzi* (Osteoglossomorpha: Osteoglossidae). Its adaptations associate neuroanatomy at different levels of the visual system with ecological and behavioural correlates and demonstrate that the visual system of this fish has adapted for simultaneous vision in air and water. The visual field is divided into three distinct areas: for viewing into the water column, into air, and for viewing the aquatic reflection from the underside of the water surface. Cone diameters in different retinal areas correlate with the differing physical constraints in the respective visual field. Retinal differentiation between the aquatic and aerial views is paralleled at different levels of the central nervous system. A diencephalic nucleus receives both direct and indirect (tectal) afferent input from only the aerial visual system and a specific type of cell in the optic tectum is preferentially distributed in the tectum processing aerial inputs. Distinctions within a single sensory system suggest that some behaviours may be organized according to visual field. For *Pantodon*, feeding is initiated by stimuli seen by the ventral hemiretina so the anatomical specializations may well play an important role as elements in a feeding circuit.

Keywords: visual system; nucleus rostrolateralis; optic tectum; retina; fusiform cell; *Pantodon buchholzi*

1. INTRODUCTION

A stereotypical vertebrate behaviour is programmatic. Such a programme is embodied by the serial and parallel neural circuits involved in devising the motor commands. The study of neuroethology addresses individual neuronal performance within a circuit whose organismic behaviour is known. In fact, the organismic role provides the interpretive framework for studying circuit behaviours. Horridge (1977) first enunciated such a principle when he coined the phrase 'mechanistic teleology': to paraphrase, it is a manner of explanation in which neuronal behaviour is part of the manifestation of a mechanism (or circuit) that represents an adaptive evolutionary structure and whose physiological properties are presumed to be efficient for a particular function.

For two reasons, the main targets of neuroethological studies are stereotyped behaviours: (i) the goal of the behaviour is well conceived in the life history of the species, and (ii) the behaviour is repetitive for an individual. These behaviours are necessary for survival of the species. Thus, the most detailed neuroethological studies have been performed on intraspecific communications, with feeding, escape and mating behaviours distant seconds, all of which are behaviours whose functions are well defined. The second requirement for this type of study is, in some fashion, for the behaviour to be more, rather than less, stereotyped. This requirement makes it possible for a specific behaviour to be a target of extended study across individuals of a single species.

The teleost fish *Pantodon buchholzi*, the African butterflyfish, inhabits an ecological niche just beneath the water surface (figure 1*a*). It preys on targets at the surface. It rarely tracks and predates on an object within the water column. For a bony fish in that niche, prey localization may be instigated by either visual or mechanoreceptive stimuli or a convergence of both.

In this niche, the visual world is unusually complicated. An eye must contend with simultaneously seeing in water and, through the water surface, into air. Retinal representation of this visual environment is even more complex (figure 1*b*). In its normal posture, the most inferior 48.6° of the retina views a 90° segment of its aerial environment, or that part of the surface that acts as the aperture through which the aerial environment is seen. The mapping of visual space within this part of its visual field is nonlinear (as constrained by Snell's sine rule), since the aerial topography is distorted by refraction through the water surface. The dorsal hemiretina views into the water column where the mapping of visual space is linear. To complicate matters, geometric optics specifies that a third part of the retina views the aquatic world as reflected from the undersurface of the water.

2. THE SPECIALIZED VISUAL SYSTEM

(a) *The specialized eye*

The eye of *Pantodon* exhibits design features that can only be interpreted as adaptations to the subsurface visual environment. A highly modified falciform process forms a horizontal shelf across the retina and protrudes into the posterior chamber to nearly the surface of the lens (figure 1*c*). The black shelf extends from the nasal pole to the optic disk and continues across the temporal retina. In the fishes' normal posture just below the water surface, this structure assumes an angle nearly appropriate for

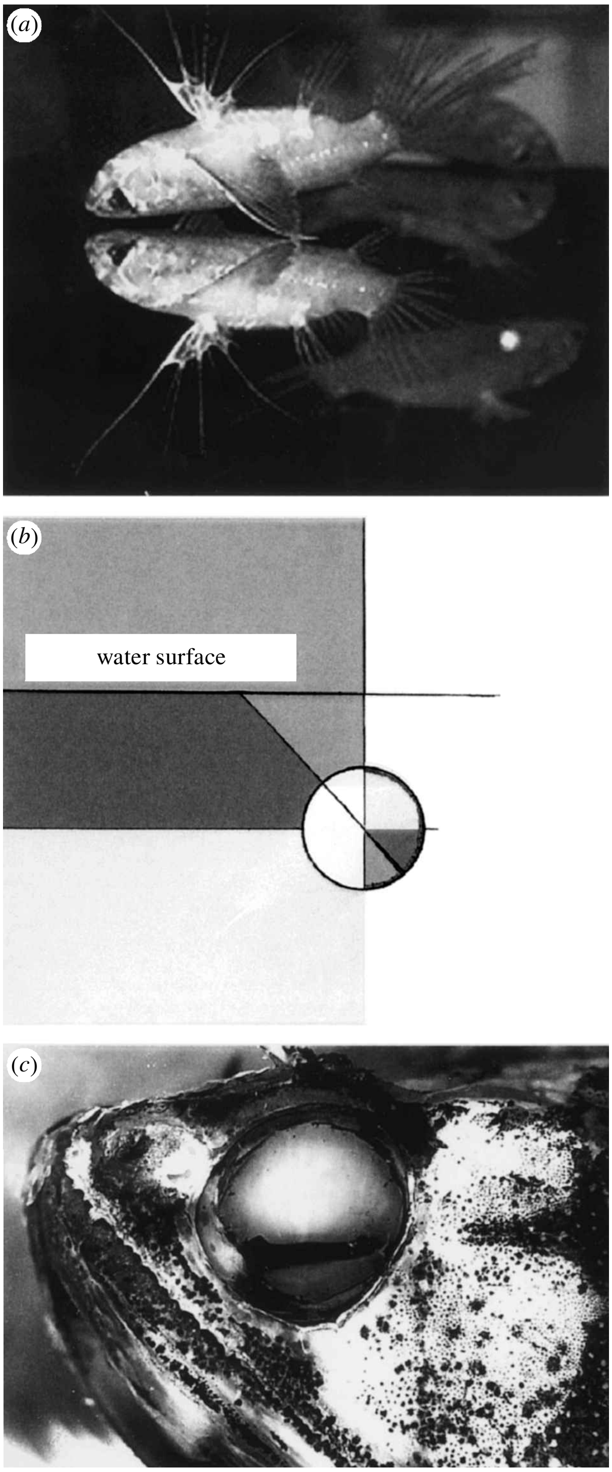

Figure 1. (a) *Pantodon buchholzi* inhabits the niche just below the water's surface. In this position, the pectoral fins and the dorsum of the head just touch the surface. (*b*) In the position illustrated in figure 1*a*, the visual world seen by the retina consists of three parts. The aquatic view (light grey) is seen by the dorsal half of the retina. The water's surface is seen by the ventral half of the retina, but the most inferior 48.6° sees a view that encompasses the aerial hemisphere (middle grey). The remainder of the retina sees the aquatic environment as reflected from the underside of the surface (dark grey). (*c*) The falciform process divides the retina near the critical angle between reflection and refraction, so that the reflected visual field is seen by small regions on either side of the falciform process.

Brewster's angle (which is the angle at which aerial light rays change from refracted to reflected). Such a bisection of retinas along a horizontal plane has been seen in some phylogenetically related (Saidel & Braford 1985) and distant (Hanyu 1959) species, all of which inhabit a niche at or near the surface during some time in the life of the species.

(b) *The retina*

To maximize visual reception, photoreceptors point towards the pupillary aperture because 'the pupillary aperture is the source of the pertinent visual stimulus' (Enoch 1981, p. 128). The wave-guide property of an individual photoreceptor explains the orientation of individual photoreceptors within a retina (Enoch 1981). As a consequence, the orientation of a photoreceptor varies with retinal position. At the posterior pole of the retina, a photoreceptor is positioned perpendicular to a retinal tangent; near the ora serrata, a photoreceptor is askew to the tangent. In between, the angle a photoreceptor makes to the local retinal tangent varies smoothly. Physiologically, the orientation of a photoreceptor towards the pupillary aperture has been termed the Stiles–Crawford effect of the first kind, and has been seen as a physiological or morphological characteristic in a wide variety of vertebrate retinas ranging from fishes and turtles to a number of mammalian species, including human (Enoch 1981; Charman 1991).

Within the *Pantodon* retina, cone orientation depends upon retinal region in a manner unlike other fish retinas (see figure 2). For both the ventral and the dorsal 'hemiretinas', the cone orientation angle is appropriate for two retinas in one eyecup. Cones in the dorsal and ventral retinas close to the falciform process (figure 2*b*,*g*) are similar to the cones in each retina near the ora serrata (figure 2*d*,*e*) in that cones describe an acute angle to a retinal tangent (but in an opposite sense). Midway between the two extreme positions (figure 2*c*,*f*), cones are perpendicular to the retinal tangent. However, both hemiretinas use the common pupil that displays no obvious adaptation.

Form discrimination, the objective of retinal vision, results in behavioural performances consequent upon discriminating different forms. Different optical media (air and water) place different optical demands on the limits of resolution that underlie this discrimination. In air, resolution is limited by diffraction effects due to the edges of the entrance pupil. Minimal resolution occurs when the central peak of an Airy disk does not overlap adjacent photoreceptors (Lythgoe 1979). In water, as Lythgoe argued (1979), the limitation on resolution is due to the loss of contrast resulting from light scatter in the aquatic environment, an environmental effect. *A priori*, the contrast constraint in water will permit no better resolution than in air and perhaps will be notably coarser. The relaxation of the constraint of pupillary diffraction in water is paralleled by an average increase in diameter of cones in the dorsal or aquatic hemiretina (compare figure 2*c* and 2*f*).

One other factor suggests the origin of this admittedly unusual retinal architecture. The cones nearest the falciform process are globular and lack an outer segment (OS; white arrow, figure 2*b*). Traversing only a few hundred

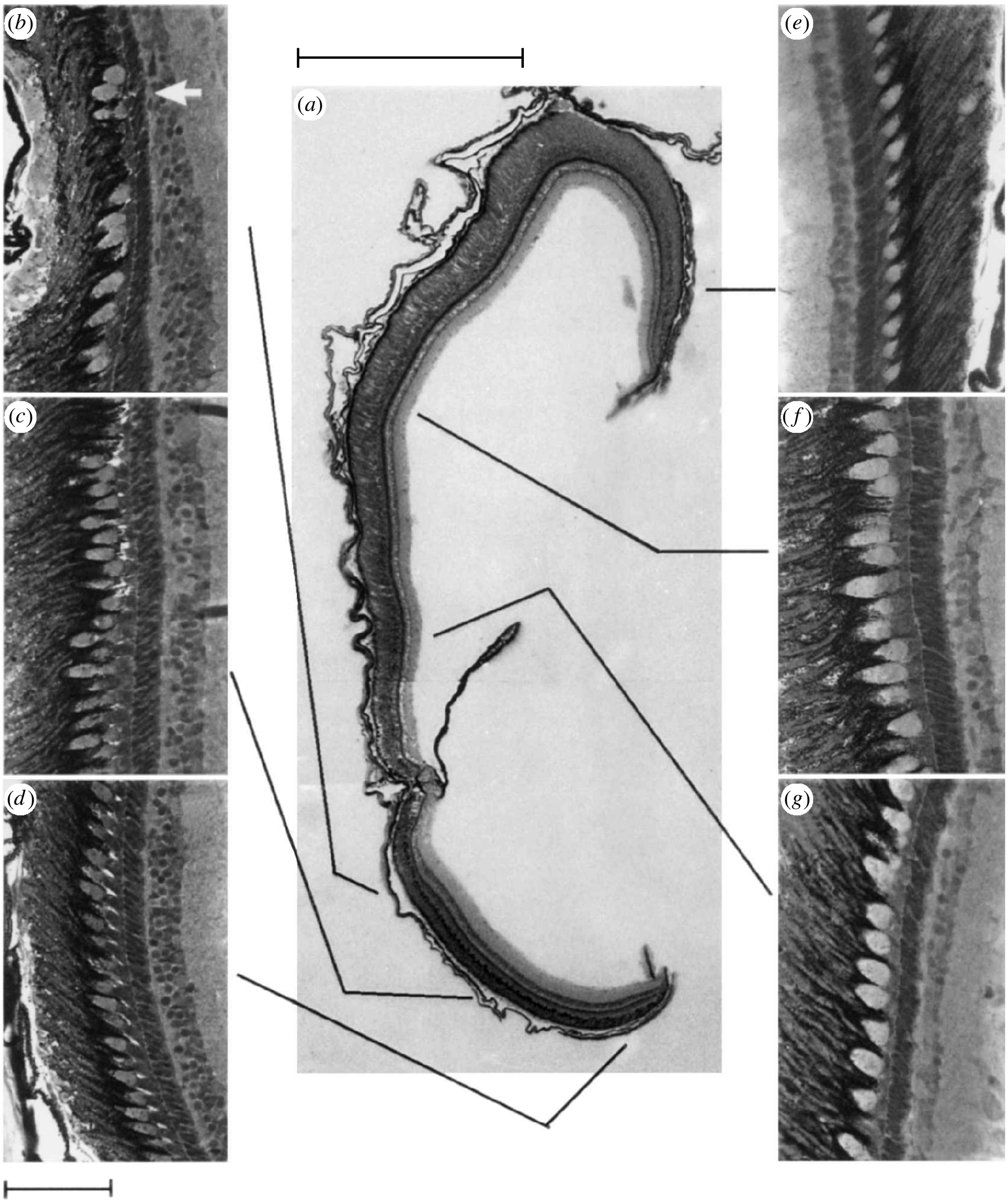

Figure 2. Cone orientation is the angle made between the longitudinal axis of the cell and the outer limiting membrane. The six inserts illustrate cone angle from different parts of a light adapted retina (*a*). The left inserts are of the ventral hemiretina; the right inserts are of the dorsal hemiretina. At mid-hemiretinas, the cones are perpendicular to the outer limiting membrane (*c*) and (*f*). At distal ends (*d*) and (*e*) and the central ends near the falciform process (*b*) and (*g*) of both hemiretinas, the cones are angled so as to point towards the pupil. Note that in (*b*), the cones closest to the falciform process (white arrow) are rounder and either lack or possess a diminutive outer segment, and they are not orientated in the same manner as slightly more peripheral cones. Scale: (*a*) 1 mm, (*b*–*g*) 50 μm.

micrometres away in the ventral retina, the cones simultaneously (i) take an angle of orientation appropriate to the periphery of a retina, (ii) progressively shrink to the characteristic small diameter in the ventral retina (figure 2*c*), and (iii) change in density (compare figure 2*b* with 2*c*). In the dorsal retina, the transition of the cones is less dramatic. The cones encountered through the transition zone become more pyramidal and OSs are clearly present. It is possible that these 'incomplete' cones lay within the visual field reflected from the underside of the water surface (figure 1*b*).

Functionally, this tripartite retina can be correlated with the optical view. The dorsal part of the retina views the aquatic visual field, a middle part of the retina views the zone of total reflection from the undersurface of the water, and the ventral part of the retina views a visual field constrained by considerations of an aerial environment. A difficulty arises with the significance of the optical view in the reflected zone. Since it is a mirror orientation with respect to the other two parts of the visual field, it would make a discontinuous or a fractured map of the entire visual field. Retinal structure alone

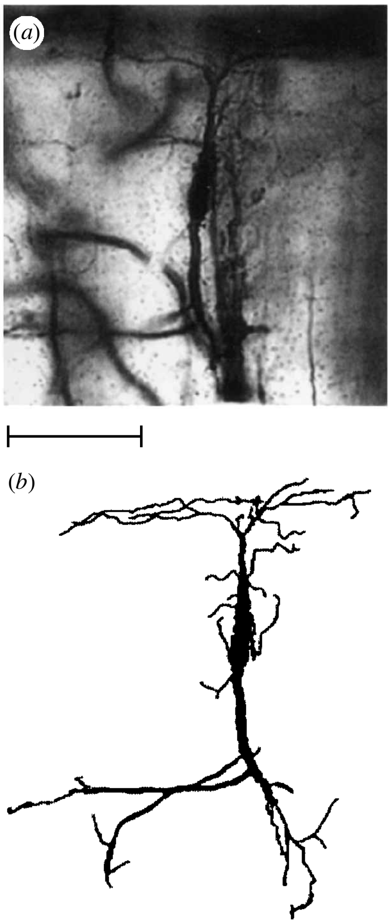

Figure 3. (*a*) A Golgi stained fusiform cell in the dorsomedial tectum and its skeletonized image (*b*) are illustrated to show the different and distinct layering of the apical and basal dendrites. Scale, 50 μm.

suggests that visibility of the reflected region of the visual field is reduced because cones lacking in or with small OSs (those around the falciform process) would have a reduced probability of light capture. Other aspects of retinal architecture support this conclusion of reduced visual function. Ganglion cells and other details of normal retinal layering are missing close to the falciform process and only gradually appear near the transition zones.

(c) *The notable visual pathway of* **Pantodon buchholzi**

Design features at the periphery of a sensory system are often reflected within the nervous system. The central visual sensory system of this fish demonstrates this principle with remarkable clarity. Retinorecipient targets of the larger dorsal retina are consistent with the visual pathway of any teleost (Butler & Saidel 1991). At least two features of the ventral retinal pathway that differ from the dorsal retinal pathway have been identified to date.

In addition to the characteristic retinorecipient targets, the ventral retina terminates in a unique diencephalic nucleus (nucleus rostrolateralis) (Saidel & Butler 1991). Significant afferent input from the dorsal retina is not present in this nucleus.

Structurally this nucleus is 'simple'. Pyriform-like cells are positioned in a cell layer medial to a large neuropil adjacent to the dorsal optic tract. The primary dendrites of these cells extend perpendicular to the long axis of the neuropil. The neuropil is composed of afferent input from both tecta but only from the dorsomedial regions. These are the regions that receive an afferent projection from the contralateral ventral retina (Saidel & Butler 1991, 1997*a*). This nucleus therefore integrates direct and indirect visual information from the aerial visual field. That this nucleus must be important for the natural behaviour of the species is indicated by its intense cytochrome oxidase expression, reflecting a remarkably high aerobic metabolic demand (Saidel & Butler 1997*b*).

If, from a neuroethological analysis of behaviour, this fish exhibits a behaviour requiring visual reception from the ventral retina that is not expressed by stimuli in the dorsal retina, then *a priori* one might expect the discriminative circuitry for such a behaviour to be restricted to the ventral retinal visual pathway. For poikilothermic vertebrates, spatio-motor transformations involve processing within the optic tectum. In *Pantodon,* these transformations refer to certain visually driven behaviours specific for only the ventral visual field and are absent from the other. *Pantodon* has a perfectly good aquatically driven optomotor reflex but lacks one from aerial stimulation (Saidel & Fabiane 1998). It is a surface feeder, voracious to prey on the surface, but tends to ignore items in the water column. The parallelism between retinal differentiation and these defined behaviours suggests that within the tectum, a discontinuity may exist in the spatial distribution of some neuronal elements involved with the different behaviourally relevant circuits. One might infer that some neural elements involved in visual processing from the ventral retina might differ compared with the neural elements processing information from the dorsal retina.

One particular tectal cell is asymmetrically distributed. The cell soma is fusiform with dendrites extending tangentially in different tectal layers (figure 2*h*). The soma is located in the middle of the stratum griseum centrale (SGC). The apical dendritic branch coincides with terminals from retinal ganglion cells at the border of the stratum opticum and the stratum fibrosum et griseum superficiale, while the basal dendrites extend into the lamina representing the border of the stratum album centrale and the SGC where mechanoreceptive input is encountered (Meek 1983). This cell type is appropriately positioned for integrating visual and mechanoreceptive inputs.

Nearly 90% of these cells, as found in Golgi and horseradish peroxidase studies (Saidel & Haynes 2000), are located within the dorsomedial tectum that processes ventral retinal information. Because of this distribution within the tectum, this type of cell is probably involved with discrimination for a behavioural function at the surface or aerial environment. The convergence of visual and lateral line inputs on it certainly suggests that this cell type is appropriately positioned to function as an element in feeding or orientation for feeding circuit. To strengthen this hypothesis, these results were compared with the distribution of this cell type in the goldfish tectum because goldfish feed from throughout its visual field. In goldfish, these cells are nearly symmetrically distributed throughout the tectum (Saidel & Haynes 2000).

3. BEHAVIOURAL CORRELATES

Behaviourally, *Pantodon* has an ability to feed in different modes. It feeds on targets directly on the surface and it will jump at a cricket suspended above the water surface. It will feed on moving targets and attack the site of water drops at the water surface in complete darkness. In addition, albeit rarely, it will feed in the water column. The programme and circuitry for target localization therefore depends upon vision, surface wave stimulation or the convergence of both. Moreover, the rarity of feeding in the water column suggests that the circuit may be present within the dorsal retinal pathway but only as a quantitatively minute fraction of the circuit present in the ventral retinal visual pathway.

The fusiform type of cell identified earlier, with the position of its dendrites and its tectal distribution, is appropriate as an essential element in a systemic circuit that includes the eye, the retina and specific areas of the brain. In the absence of knowledge about the Stiles–Crawford effect, photoreceptor orientation would simply be an interesting observation. In the absence of knowledge of the visual field and its retinal mapping, the horizontal falciform process across the fundus of the retina would be a curious structure. In the absence of details about sensory mapping in the tectum, the fusiform cell would reflect an interesting convergence of two senses performed by an asymmetrically distributed type of cell. The interpretation of these features in the context of the fishes' behaviour adds a historical and/or evolutionary context to the construction of a behaviourally relevant circuit. No known benthic or pelagic species exhibits this constellation of features—only species at the surface. That conclusion alone argues that this circuit represents a successful evolutionary adaptation for this fish in its natural niche.

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