Small-field, binocular neurons in the superficial layers of the frog optic tectum

BY D. J. FINCH AND T. S. COLLETT

School of Biology, University of Sussex, Brighton BN1 9QG, U.K.

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Binocular neurons with receptive fields about 5° across were recorded just beneath the pia. Most of them responded to dark stimuli in the lower half of their receptive field and to light stimuli above. There was almost no vertical disparity between the left and right fields and the modal value of the horizontal disparity of the population of cells was 1.7°. Because frogs do not verge their eyes it is possible to calculate at what distance the receptive fields through the two eyes are superimposed. This calculation suggests that the neurons are tuned to detect features in the external world about 50 cm away. This is too far for the neurons to be involved in the frog's everyday distance vision. It is more likely that they are concerned with assessing the vertical position of a horizontal surface.

1. Introduction

Many frogs and toads can measure the distance of their prey over a range of about 30 cm using either monocular or binocular cues (Ingle 1976; Collett 1977; Jordan et al. 1980) to do so. Experiments with prisms suggest that within their binocular field toads normally compute the horizontal disparity of the prey image in the two eyes and use this information to gauge distance (Collett 1977). Since anurans do not make vergence eye movements (Grüsser & Grüsser-Cornehls 1976; Grobstein et al. 1980), there can be a direct translation of disparity cues into distance.

The optic tectum is considered to be essential for mediating prey capture (Ingle 1970) and receives input from both eyes. Each tectum has a major, direct input from the contralateral eye (Levine 1980), while the primary inputs from the ipsilateral eye are indirect, coming both from thalamic nuclei (Trachtenberg & Ingle 1974) and from the contralateral tectum via the nucleus isthmi (Grobstein et al. 1978; Gruberg & Udin 1978). The inputs from both eyes are mapped retinotopically and in register onto the surface of the tectum (Gaze & Jacobson 1962; Liege et al. 1972; Grobstein et al. 1980), giving a potential anatomical substrate for measuring disparities.

We were interested, therefore, in examining the properties of tectal neurons with binocular receptive fields in order to compare their behaviour with that of disparity-sensitive neurons which have been recorded in the striate cortex of mammals (cat, Barlow et al. 1967; sheep, Clarke et al. 1976; monkey, Poggio & Fischer 1977) and in the Wulst of the owl (Pettigrew 1979), and to assess their possible role in distance vision. We describe here the receptive field properties of a hitherto unreported class of tectal neurons. Indeed, this is the first published
account of binocular neurons with small receptive fields in the amphibian tectum, though small-field cells have been encountered previously in deeper tectal layers (P. Grobstein, personal communication).

2. Methods

*Rana pipiens* were anaesthetized with tricaine methane sulphonate (MS 222) and the cranium, meninges and dura were removed sufficiently to expose the tectum. After the nictating membrane had been cut, the cornea was covered with silicone fluid (Dow Corning 200; 600 St) to keep it optically clear. During the experiment MS 222 was infused through a subdermal cannula to provide a steady level of anaesthesia, and the frog was kept oxygenated and tranquilized by an equal mixture of warm, moist N₂O and O₂ flowing through a narrow nylon tube into its buccal cavity at about 40 cm³ min⁻¹. On occasions the brain moved too much to permit stable recordings. The cranial cavity was then filled with warm, liquid gelatin (Sigma, Type 1) which, when set, immobilized the brain.

Action potentials were recorded with glass-covered, tungsten microelectrodes constructed in the following way. Tungsten wire 5–6 μm in diameter was inserted into 7 cm lengths of capillary tubing (1.5 mm o.d., 0.7 mm i.d.). Microelectrodes were pulled from these lengths of tubing on a conventional puller. Each length resulted in one usable electrode with a length of tungsten wire protruding beyond the tip of the glass. The wire was then etched electrolytically under a compound microscope in a drop of sodium nitrite held in a platinum loop.

The frog was carefully positioned so that its jaw-line was horizontal. It faced a back-projection screen 57 cm away. The origin on the screen was taken to be its point of intersection with a line defined by the intersection of the frog’s midsaggital plane with a horizontal plane passing through the middle of its eyes. The pressure of gas inside the buccal cavity seemed to help keep the frog’s eyes in their normal position with respect to the head. The position of the eyes in the head with respect to the origin on the screen was measured in terms of the position of the optic nerve head viewed through a sighting tube mounted on two protractors. The optic nerve head was illuminated by light diffusing through the brain from a beam of light directed either onto the brain in experimental preparations or onto the top of the head in intact animals examined for comparison. The nerve head could then be seen glowing when the eye was viewed from the appropriate direction. Its horizontal position was reasonably constant (range 46–49.5⁰) from preparation to preparation and agreed with the figures given by Grobstein *et al.* (1980). We concur with their conclusion that frogs have a standard eye position from which phasic deviations can be induced by optokinetic or vestibular reflexes.

In the superficial layers, our electrodes rarely sampled single cells in isolation; usually we recorded from two or three at once. Individual units were identified by the characteristic shapes of their action potentials. A representative action potential was frozen on one beam of a dual beam storage oscilloscope and the profile of this standard potential compared with responses to visual stimuli stored on the other beam. Since the cells were not spontaneously active we could plot their
Opaque occluders were placed in front of one or other eye in order that the receptive fields for each eye might be plotted separately. Fields were mapped once with 1.5° light and once with 1.5° dark spots, jiggled very slightly. When a response was evoked we recorded the position of the centre of the spot on the projection screen. The intensity of the bright spot measured at the screen was 5.3 lx against a 0.25 lx background, and for dark spots the intensities of target and ground were reversed.

Figure 1. Receptive field plots of superficial tectal binocular neurons. Symbols show where a response was evoked by dark or light 1.5° spots. Circles: field plotted through right eye. Triangles: field through left eye. (a) In both fields dark spots evoke activity in the lower half and light spots in the upper half. (b) Right field is as (a), but the left field is less clearly organized. Fields through the two eyes are almost superimposed, but to avoid clutter they have been drawn separately.

3. Results

Electrodes were placed on the surface of the right tectum so as to sample neurons with frontally located receptive fields. The centres of the fields of all the cells lay within an area bounded below by the equator and above by a 22° line of latitude. The horizontal limits were lines of longitude 7° to the left and 15° to the right of the meridian. The units to be described were recorded immediately the electrode penetrated the tectum to a depth of about 100 μm.

The sizes of the ipsilateral receptive fields of the 38 binocular neurons were generally a little larger than the contralateral. The mean horizontal and vertical extents of the ipsilateral fields were respectively 5.4° (s.d. 1.47°) and 5.4° (s.d. 1.49°). The contralateral fields extended horizontally 4.3° (s.d. 0.97°) and vertically 4.8° (s.d. 1.08°).

Most cells responded only to dark spots in the bottom half of their receptive fields and to light spots above ( figure 1a). The receptive fields of some cells, however, were less clearly spatially segregated ( figure 1b left field). Their response to dark
spots was limited to the lower half of the field, but light spots evoked activity throughout. A few cells showed no spatial segregation at all, some responding to dark or light spots (■), others just to light (□), and yet others to dark (□). Table 1 categorizes these binocular cells accordingly. The cells of the table are not exclusive. The unit of figure 1a, for instance, contributes an entry to each cell of the top row, and the unit of figure 1b contributes to the first cell of the top row and to the second cell of the second row.

![Figure 2](http://rspb.royalsocietypublishing.org/)  
**Figure 2.** Distribution of disparities between fields plotted through left and right eyes for a population of 38 binocular neurons. (a) Vertical disparity defined for each unit as the difference in height between the centres of the left and right fields. (b) Horizontal disparity defined by α in inset.

**Table 1. Classification of binocular units showing number recorded in each category**

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<th>Ipsilateral field</th>
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<th>Binocular field</th>
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In addition to responding to spots, 66% of the binocular units were also activated by the edge between a dark and light area extending across the whole 60° of the screen. For a response to be evoked the dark side had to be below the light, the edge had to fall precisely on the boundary between the dark and light regions of the field, and it had to be oriented within about 30° of the horizontal. The unit became active as the edge was moved into position and it sometimes continued to discharge for several seconds when the edge was held stationary there.

Our major concern, though, was with the relative positions of the left and right receptive fields and we found them to be almost in register. For each neuron we determined the differences in the height and in the horizontal position of the centres of the left and right receptive fields. Figure 2a plots the distribution of vertical disparities, showing that they are essentially zero. The distribution of horizontal disparities (defined as $\alpha$ in figure 2b) has a modal value of about 1.7° and a scatter that is commensurate with the variation in eye position that we measured.

**Discussion**

Anurans are known to be able to judge distances precisely over a range of about 30 cm. Thus, grass frogs jump accurately at their prey provided that they are no further away than about 25 cm (Collett & Harkness 1982). Both toads (*Bufo bufo*) and frogs (*Rana pipiens*) select prey according to its real size and in both species this size constancy breaks down for viewing distances greater than about 20 cm.
Toads (*Bufo bufo*) will leap over chasms so long as they are no wider than about 20 cm (Lock & Collett 1979). The population of neurons described here would be of little help in any of these tasks.

Since a frog’s eyes are held in a standard position and do not verge, binocular disparity can be translated directly into distance, that is we can calculate at what distance the receptive fields corresponding to a given binocular disparity will be superimposed. This relation is shown in figure 3 for frogs like ours with 1.5 cm separation between the pupils. The shaded area indicates the disparity range of the population of binocular neurons. The largest recorded value of $\alpha$ was 3.4°, which is equivalent to a distance of 25 cm. However, the modal value of the distribution of disparities (1.7°) is probably a more accurate estimate of the kinds of distances that these cells might monitor, and this suggests that the neurons are tuned to detect objects no closer than 50 cm.

These calculations are based solely upon differences in receptive field positions in the two eyes. Thus, we do not know whether there are inhibitory interactions that might enhance the neurons’ ability to discriminate disparities, so that their response is limited to objects lying within a narrow range of distances, as in the monkey (Poggio & Fischer 1977). However, the powerful response of some neurons to extended edges suggests that these cells are probably not part of a system for providing precise information about horizontal disparities. Their receptive field organization makes it more likely that they are designed to assess the vertical position of the horizon or the top of some object seen against the sky. Another possibility (H. B. Barlow, F.R.S., personal communication) is that they supply a signal for aligning the two eyes vertically. It remains to be seen whether other binocular cells in tectum (Fite 1969) or thalamus (Keating & Kennard 1976) might provide suitable information for measuring close distances. It should perhaps be pointed out that the assessment of local disparities is not the only way in which a frog might use binocular information to compute distance.

Finally, some comment is needed concerning the superficial location of these small-field binocular neurons. The upper layers of the tectum contain few cell bodies and we suspect that we have been recording from dendritic processes. Interestingly, it is a region rich in axon terminals from both the ipsilateral and contralateral nucleus isthmi (Gruberg & Lettvin 1980) so that the binocular units may receive indirect input not only from ipsilateral but also from contralateral retina via the two nuclei isthmi.

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References


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