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The psychology of the frog's retina

H B Barlow, 11 July 1952

Editor's Note: This is the text, hitherto unpublished, of a paper given to the Experimental Psychology Group at its Cambridge Meeting, 10-11 July 1952 (v. Quarterly Journal, 1953, vol. 5, p 39). It is reproduced from Horace Barlow's original handwritten manuscript. Professor Barlow has kindly supplied a few missing details (in italics and square brackets) and has added an historical note.

1. Introduction

I am actually going to talk about the neurophysiology of the retina, but I don't think I am being a complete fraud in pretending that it has something to do with psychology. What I have to say seems to me to be relevant in two ways: First, the explanation, partial or complete, of any feature of sensation is of interest to you, and of course the retina is responsible for some features of sensation. I hope to show that simultaneous contrast and some illusions are the simple result of the neurological organisation of the retina, but I also hope to show that, in the frog, the properties of its retina determine a large fraction of its visual behaviour. If you compare the visual behaviour of a frog with that of a rather similar animal, like the toad, you find certain differences; for example, they both feed largely by sight but the frog prefers flies, where the toad prefers grubs. I think this "preference" is the simple result of differences between the two retinæ. Give a toad a frog's retina, and it would have the frog's preferences.

The second way in which physiology might help hardly needs pointing out. You try and analyze complicated behaviour and you find it necessary to introduce concepts such as recognition, memory, learning. It must be obvious to you that you are getting it all wrong, just as it was obvious to more intelligent doctors that explanations of typhoid without knowing about the typhoid bacillus were all wrong. Neurophysiologists are, as it were, investigating the bacteria, and it is partly up to you to decide if any of our results help in understanding the disease.

2. Visual behaviour, neuroanatomy and retinal structure

Most of the experimental results I shall describe were done on the frog's eye, and I shall just remind you of the anatomy of the visual pathway in the frog. But first perhaps I had better remind you of the visual reactions that frogs show. Yerkes [1903] worked on this, and it is very simple; they only use their eyes in feeding, and in escaping from large moving objects. They do not apparently depend on visual cues in

finding their way about in their habitat, nor in mating. [Added note - This is now known to be wrong. Amphibians can use their eyes in quite sophisticated ways to navigate in their environment. See Collett 1982]

When a frog sees something, it has not got a very complicated decision to make. It only has to decide whether to escape from it, or eat it, or do nothing about it.

Slide 1 shows the structures which might be responsible for making the decision.

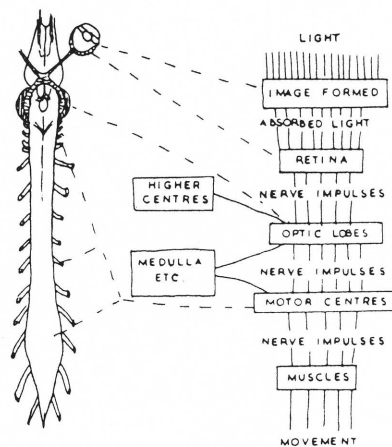
I shall try and argue that the decision whether to run away, to give chase, or simply to stick out the tongue and catch the object, is virtually made in the retina: the rest of the nervous system is there to execute orders received from the retina - unless of course the frog has something more important on its mind, such as mating. This is not a very big claim; after all, if I put a drop of fluid on a frog's back, sometimes it will wipe it off, sometimes it will not - it depends whether the fluid was hydrochloric acid or water. The decision in this case is made by the sensory endings in the skin.

This slide shows the structures we are dealing with. There are about 300,000 receptors in which light is absorbed, and about 30,000 ganglion cells with nerve fibres leading to the brain. [Note that this figure is now known to be too low because the early counts failed to include the large number of non-myelinated fibres]

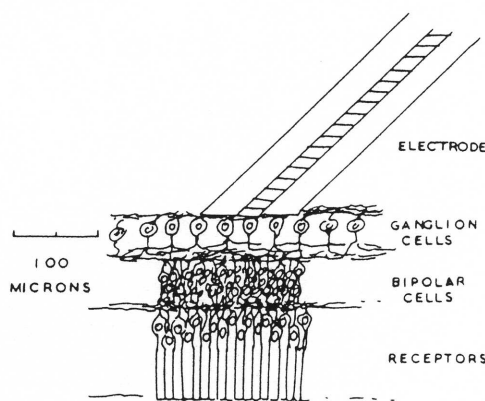
Embryologically and histologically the retina is just like the central nervous system, and I suggest that functionally it is also C.N.S., in contrast to the view that it is simply a transducer for copying a pattern of light and shade into a similar pattern of nerve impulses.

3 Technique

You cut out the eye, remove the optics and vitreous, and apply the electrode. This enables you to isolate activity in a single retinal ganglion cell as shown in slide 2.



Slide 1. The sequence of events is as follows: light enters the eye, excites the photoreceptors and optic nerve fibres, and messages are sent to the superior colliculus, and ultimately to the spinal cord where the appropriate muscular actions are initiated and controlled.



Slide 2. Diagram of the frog's retina with the transparent plastic coated electrode placed on the ganglion cell layer to pick up action potentials. Approximately to scale.

