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Two Visual Systems in the Frog

Abstract. *After unilateral removal of the optic tectum in frogs, the cut optic tract regenerates to the remaining ipsilateral tectum. Although the orienting movements elicited by moving objects (food or threats) are now directed mirror-symmetrically to normal responses, these frogs correctly localize stationary objects as barriers. Apparently, thalamic and tectal visual mechanisms can operate independently.*

One of the primary tasks for the neurobehaviorist is to dissociate components of behavior that are generated by distinct elements of the nervous system. Although the sensory systems of vertebrates have considerable anatomical and functional independence, attempts to disentangle behavioral functions within a particular system have produced few definitive conclusions at any level of vertebrate phylogeny. Schneider (*1*) has provided new support for the belief that the mammalian visual cortex and superior colliculus (or optic tectum) have distinct behavioral functions. In the golden hamster, lesions of the striate cortex produced pattern discrimination deficits, while tectal ablations abolished visually elicited turning of the head toward interesting objects, such as food. Because the striate cortex and optic tectum receive information from independent retinofugal pathways, Schneider labeled the geniculostriate and tectal pathways as two visual systems. In the study reported here, I have sought to dissociate certain behavioral functions of the frog's visual thalamus from those of the optic tectum by using natural orienting behaviors—rather than discrimination training methods. It appears from these results that tectum and thalamus can mediate spatial localizing responses which are morphologically identical but are elicited by different classes of visual stimuli.

The first set of observations that seemed to dissociate two types of visual function were made on four specimens of *Rana pipiens*, in each of which one tectal hemisphere had been totally removed by use of a microknife, hook, and aspiration. As histological checks later showed, each frog had lost all of the tectum plus some of the immediately subjacent tegmental region. These subjects were typical of more than 20 unitectal frogs in that they vigorously pursued mealworms or dummy prey objects viewed by the eye contralateral to the intact tectum, but totally ignored prey moving within the monocular field contralateral to the damaged side. As Bechterew (*2*) reported in the 19th century, such blindness also included failure to jump away or duck the head in response to a looming dark object. Unitectal frogs reacted to a motor-driven, black "looming" disk (~ 10 cm wide) moved briskly through 30 cm to within 3 cm of the normal eye in 49 of 60 trials, but never reacted when the stimulus was confined to the field of the "bad eye." Yet the same subjects readily jumped away from a light touch of the limbs on the "blind" side. With respect to food pursuit and avoidance behavior, tectal ablation in the frog produces a "blindness" very similar to that reported for the hamster (*1*) or the tree shrew (*3*) after total removal of the optic tectum.

Although these unitectal frogs did appear blind by such criteria, they could nevertheless discriminate the presence of stationary visual objects, just as the hamster and tree shrew could after ablation of the optic tectum. Five frogs deprived of the right tectum consistently avoided stationary grid barriers after the "good eye" had been sewn tightly shut. By contrast, when both eyes were sewn shut and a frog was motivated to escape a light touch or pinch of the left heel by a long pair of tweezers, all jumps were made

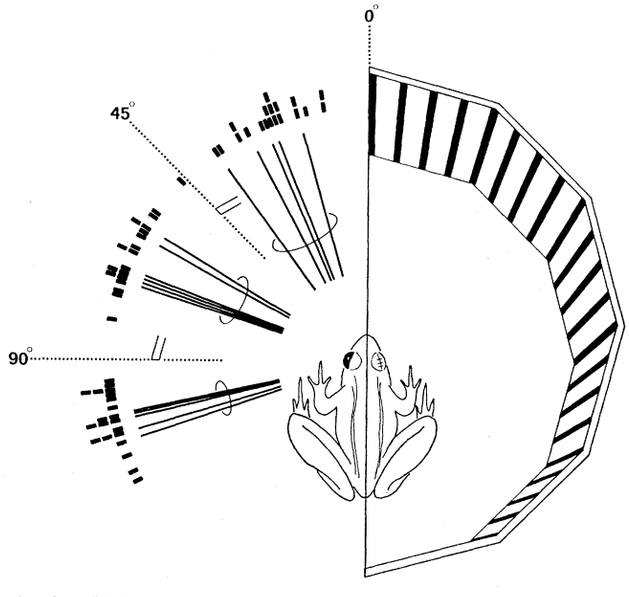

Fig. 1. Results of the barrier avoidance tests for five unitectal frogs using the eye projecting to the injured half of the brain. The visible edge of the 15-cm-high barrier was set at either 0°, 45°, or 90°, and the avoidance jump directions were measured from stopped cine projections. The angle by which the frog cleared the barrier is represented here for each trial by a vertical black rectangle to the left of the barrier edge. Group data are presented as radial histograms, and the responses of one individual are shown by three sets of radial lines, corresponding to the three barrier locations.

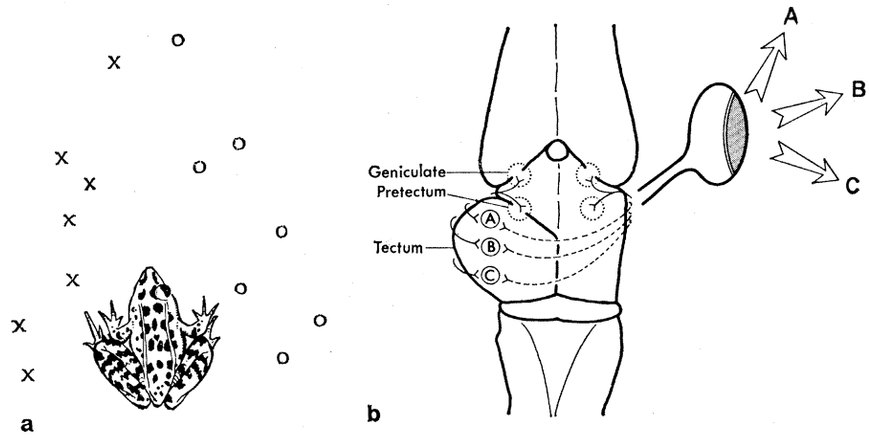

Fig. 2. (a) Illustration of the mirror-symmetrical relation between the location of a prey stimulus (head of a moving worm) and the frog's corresponding snap (center of the tongue print). Several tracings from 16-mm cine projections were superimposed so that the prey location (circles) and tongue direction (crosses) could be marked in relation to the frog's body location before each response. (b) Schematic illustration of optic tract regeneration to the ipsilateral tectum. (The exact route of fiber regrowth is unknown.) These fibers remap a topographic projection on the ipsilateral tectum, which overlaps the normal contralateral projection. Ipsilateral input to locus *A*, *B*, or *C* elicits a response in visual direction *A*, *B*, or *C*, respectively, as if stimuli were seen in these locations via the contralateral eye. Note that retinofugal input to thalamic nuclei remains intact on the injured side.

directly forward so that the frog always collided with a frontal barrier. A successful avoidance response, where the frog used the eye opposite the injured half of the brain, consisted of a jump of 15 to 30 cm directed just lateral to the visible edge of the barrier, which consisted of a hemicylindrical Lucite structure covered with vertical black stripes 3 mm wide (Fig. 1). This barrier was placed with the frog's head approximately centered and so that the visible edge lay on the rostral midline, or at either 45° or 90° within the left visual field. As these positions were randomly interchanged, a 16-mm film record was made of the frog's orientation just before and just after a reorienting or avoidance jump was made. Usually frogs turned or jumped away from the barrier within 10 seconds when the left heel was lightly pinched. Each frog was given five to eight trials at each of the three barrier positions, and the test was stopped as the particular frog became refractory to moderate tactile stimulation.

In order to objectively describe this avoidance behavior, single-frame cine projections were traced to record the frog's head position and the barrier position before and after each jump. For this analysis, reorienting responses were not measured (although frogs turned away from the barrier in all but one instance). The lines connecting the midpoint of the frog's head to (i) the barrier edge before the frog jumped and (ii) the midpoint of the head after the frog jumped past the barrier were traced out, and the angle subtended by these was measured. The frog's directional consistency was thus scored in terms of the distribution of angular distances by which they missed the barrier. Jumps were scored only when the barrier was within 10° of the intended location (0°, 45°, or 90° from the midline). For these three barrier locations, the mean jump clearances were 23.2°, 21.8°, and 14.3°, respectively, as shown by the radial histograms in Fig. 1. Since there was no overlap between the three sets of responses (even though group data were used), I conclude that monocular frogs without a contralateral optic tectum can quite accurately localize the terminal edge of such a barrier. Other informal tests indicated that these frogs can leap hurdles and duck through small apertures in an apparently normal manner.

Although these tests do seem to establish that the contralateral optic tectum is not necessary for avoidance of stationary barriers, it remains possible that input to the tectum normally does participate in this type of behavior. However, reason to doubt this possibility was obtained in an unexpected manner, after I discovered that fibers from the bad eye would eventually regenerate to the remaining ipsilateral tectal hemisphere in most cases. When tested 6 to 8 months after surgery, 12 frogs could be induced to snap when objects were moved within the part of the field where they were formerly blind to motion. However, these responses were always directed toward a location nearly mirror-symmetrical to the location of the stimulus, just as Sperry (*4*) has described for frogs with surgically uncrossed optic nerves. Figure 2a shows the results of an analysis of single frames from a film of one frog's responses.

Recordings from the remaining optic tectum with tungsten or platinum-iridium microelectrodes showed conclusively that the regenerated portion of the optic tract had indeed re-formed a topographical projection over the dorsal surface of the ipsilateral tectum. For five suitable subjects, each of more than 30 penetrations through the dorsal rostral tectum showed that receptive fields of units activated via opposite eyes at any particular recording point were always mirror-symmetrically located. The usual succession of retinofugal fiber terminals of classes 1, 2, and 3 was found during penetration of the superficial neuropil, although the spread of receptive fields of individual units was often unusually wide. Despite the fact that retinotectal input (and snapping behavior) was remapped via the ipsilateral eye in a mirror-symmetrical fashion, four frogs that were given the standard monocular barrier tests always oriented in the normal direction while jumping past the barrier edge. These results reinforced the suggestion that two independent visual systems mediate localization of prey stimuli and of stationary barriers, since the same frog can respond in opposite directions depending on the nature of the eliciting stimulus.

So far the best evidence indicates that visual input to the pretectal region of the caudal thalamus mediates barrier avoidance behavior. In the toad some single neurons within this region are selectively responsive to large stationary objects (*5*)—a result confirmed by my unpublished studies on the frog's caudal thalamus. Furthermore, in replicating the findings of Ewert (*6*) that caudal thalamic lesions produce toads that are disinhibited in their feeding behavior toward prey objects, I noticed that this deficit is usually accompanied by an inability to sidestep stationary barriers set in the toad's path during pursuit of moving

objects. However, no data from either recording or lesion studies define the possible role of the retinal projection to the anterior thalamic neuropil in barrier avoidance.

There is already some evidence that functions of retinothalamic and retinotectal fibers can be dissociated in the shark, where a simple pattern discrimination suffers more from removal of the telencephalon (*7*) than from tectal ablation (*8*). In these demonstrations the discrimination stimuli were vertical and horizontal stripes—stimuli quite comparable to the grid barrier detected by the tectally injured frog. In fact, normal frogs spontaneously discriminate between vertical and horizontal grids and between vertical and horizontal apertures (*9*). While comparisons of visual mechanisms in the frog and in mammals are still tenuous, my distinction between motion detection by the tectum and stationary edge detection by the thalamus in frogs does parallel the pervasive distinction between sensitivity to motion and sensitivity to edge orientation in the tectal and thalamocortical systems in mammals. In support of this hypothesis, Casagrande (*10*) observes that tree shrews with tectal ablations also fail to localize food objects but, like frogs, are surprisingly successful in negotiating stationary barriers and darting through holes. These new data on sharks, frogs, and tree shrews support the view that the anatomical similarities in retinofugal patterns from fish to primate (*11*) provide the foundations for a basic set of visual functions which have been elaborated but not reconstructed during evolution.

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Enhanced Protein Adsorption at the Solid-Solution Interface: Dependence on Surface Charge

Abstract. *By the use of infrared internal reflection spectroelectrochemistry, it has been possible to observe an enhanced adsorption of porcine fibrinogen onto a germanium surface at potentials more positive than −200 millivolts relative to a saturated calomel electrode. The enhanced adsorption was observed directly at the interface between the solid and the aqueous solution.*

Several investigators (*1*) have demonstrated that the formation of a protein film precedes platelet adhesion during thrombogenesis on foreign surfaces. Baier and his co-workers (*2*) contend that the protein layer transmits the particular characteristics of a given surface into the blood, whereas other investigators (*3*) suggest that the free energy of the surface is responsible for its thrombogenicity. Sawyer and his co-workers (*4*) have observed that surfaces with a uniform positive charge attract the negatively charged blood platelets and proteins. Many empirical in vivo studies have been carried out in attempts to clarify this phenomenon, with substantive data (*5*) indicating that the surface charge does play an important role in formation of thrombus.

We report evidence here in support of the theory that a relatively positive charge at the surface of a germanium electrode substantially enhances the extent of adsorption of fibrinogen from aqueous saline solution. We measured the adsorption of fibrinogen in vitro by infrared internal reflection spectroscopy, using a germanium prism as both the electrode and the internal reflection element.

Internal reflection spectroscopy has been discussed in detail by Harrick (*6*), and the technique of simultaneous electrochemistry and internal reflection spectroscopy has been described in several papers (*7*, *8*). In this study we employed a Perkin-Elmer model 180 infrared spectrophotometer, with the manufacturer's internal reflection accessory. Germanium prisms (52.5 by 20 by 2 mm and 52.5 by 20 by 1 mm, Harrick Scientific Corporation) provided, respectively, 25 and 50 internal reflections at an angle of incidence of 45°. Because of cell geometry, only 11 and 22, respectively, of these reflections were actually at the germanium-solution interface. We constructed a two-compartment Teflon electrolysis cell similar to that described by Tallant and Evans (*8*), with the following modifications: (i) the counter electrode was a 10-cm platinum coil; (ii) electrical contact with the germanium prism was obtained by clamping a piece of aluminum foil to the entire "back" face of the prism (this was done to eliminate the possibility of variations in the potential from the edge to the center of the electrode); and (iii) the reference electrode was a conventional saturated calomel electrode (SCE), connected to the working electrode compartment by a 16-gauge Teflon catheter filled with saline agar gel. A potentiostat (Wenking model 70TS1) was used to maintain the desired potential, which was measured with an electrometer (Keithley model 602).

The germanium prism was cleaned before use by rinsing with concentrated HF, and then it was placed in a radio-frequency gas discharge for approximately 30 minutes. The solutions were prepared from doubly distilled, deionized water and reagent grade NaCl. Porcine fibrinogen (60 percent clottable) was obtained from Miles Laboratories and kept at 5°C until used. For the experiments reported below the solutions used consisted of 0.15*M* NaCl and 0.4 percent (by weight) fibrinogen in 0.15*M* NaCl solution. All potentials are relative to those of a SCE unless otherwise stated.

Figure 1 reproduces 14 infrared internal reflection spectra. The spectra are shown in the linear absorbance mode, and in each case the spectrum was manually displaced upward without changing the relative magnitude of the absorbance value. The peaks at 1205 and 1150 cm^{-1} are due to the Teflon, and the little blip at 1486 cm^{-1} is due to a filter change. In Fig. 1 the amide I band at 1650 cm^{-1} is naturally obscured by the water peak at 1640 cm^{-1} and so the amide II band at 1540 cm^{-1} is the "indicator" peak. Other protein absorption bands occur from 1400 to 1000 cm^{-1}, but they are quite diffuse.

The 14 spectra of Fig. 1 may be described as follows. The bottom spectrum, spectrum 1, is the germanium-cell base line. Spectrum 2 was taken