trained eye, color information must be relayed by the commissural system more effectively than is the relevant information on pattern.

These results indicate that two processes of visual coding must underlie the learning of discrimination in this experiment. However, in absence of a specific control for differences in apparent brightness of the red and green colors, I cannot state with finality that hue alone comprised the second coding dimension. When differences in brightness are controlled, goldfish do transfer interocularly a discrimination between red and green stimuli on the basis of hue (*11*). Color probably was the dimension controlling behavior in my study also, since goldfish "generalize" without error from discrimination between solid red and solid green to discrimination between red-on-white and green-on-white patterns, despite the great increase in luminous flux (*12*).

The idea that interocular transfer of color discrimination is generally superior to transfer of an equally discriminable pattern discrimination depends on further exploration with other appropriate color-pattern combinations. Final proof that two visual coding processes (specified by behavioral analysis) in fact utilize different commissural pathways requires evidence obtained either from direct surgical disruption of the pathways, or from electrophysiological recording within the neural substrate of transfer.

Use of the "conflict test" method has proved effective for analyzing interocular transfer of ability to discriminate visually. The fact that the rank order of discriminability of two visual dimensions can be reversed between eye and eye provides a tool for disentangling other dimensions of the visual world. For example, among pattern discriminations that differ along two possible dimensions, interhemispheric transfer may impose a selective bias such that one dimension transfers more readily than the other. Because the commissural systems may sometimes act as "filters," appropriate interocular generalization tests can reveal distinct coding processes which are inextricably mixed during the more familiar binocular generalization paradigms.

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Vocalization Evoked from the Optic Lobe of a Songbird

Abstract. *Vocalizations from songbirds have been evoked by electrical stimulation of the torus. These vocalizations resemble the normal alarm and scolding calls of the species. The torus of the birds appears to correspond functionally and anatomically to the mammalian central gray matter.*

The rostral central gray matter of the midbrain has been found by stimulation of both restrained (*1*) and freely moving (*2*) cats and monkeys to be important in the vocal expression of threat behavior (*3*). Damage to the central gray matter can result in partial or complete loss of emotional vocalization in cats (*4, 5*) and dogs (*6*). That it has "motivational" importance has been shown by passive avoidance of (*7*) and escape from (*8*) stimulation of the central gray matter in cats and by decreases in conditioned avoidance responses to noxious stimuli after lesions in cats (*5*) and rats (*9*). The important role of the central gray matter in emotional vocalization in mammals suggests that it might play a corresponding role in the vocalization of birds. The experiments below delineate an area in the avian midbrain from which vocalizations can be evoked by electrical stimulation. These results, together with physiological and neuroanatomical considerations, suggest that the torus semicircularis of birds corresponds to the central gray matter of mammals.

A species of the suborder Passeres ("songbirds") was chosen because this group has an advanced sound-production apparatus (*10*) and is renowned for its vocalizations. Adult male red-winged blackbirds (*Agelaius phoeniceus*) obtained from the marshes around Rochester, New York, were used. Birds were placed in a restraining device that prevented wing and leg movements from exerting pressure on the head holder. After application of a local anesthetic to the ears and crown, the birds were placed in a stereotaxic instrument in such a way that the bill could be opened and closed freely. Electrodes, 0.2 mm in diameter, were made of nichrome steel insulated with enamel and Insl-X; they were exposed only at the pointed tips. A Wyss stimulator (*11*) was used for monopolar stimulation with the indifferent electrode being a steel screw in the skull anterior to the brain. A frequency of 30 pulses per second was employed, with a biphasic pulse of 3.5-msec rising time and 7.0-msec falling time (negative phase). The electrode was lowered through the brain, and at 1-mm intervals a 500-μa current was applied for 30 seconds. When a responsive area was found, the interval was shortened to 0.1 or 0.2 mm and the vertical extent of the area was usually determined.

Vocalizations were elicited from an area beneath the optic tectum including the torus semicircularis (*12*) and the underlying gray matter (*13*). The responsive area was roughly triangular in cross section at its thickest part, ranging in vertical extent from 3.0 mm at the medial end of the torus to a fraction of a millimeter at its most lateral extent. Calls were obtained from stimulation of almost the entire anteroposterior extent of the torus, about 3.0 mm. In the torus, all of 44 points distributed along seven electrode tracks in five birds yielded vocalizations; no points tested in the torus failed to yield vocalizations. Of all points tested, thresholds were lowest (20 to 30 μa) in the center and lower border of the torus (as in Fig. 1) and increased with more ventral, medial, and lateral positions of the electrodes in the torus or outside it. In the gray matter underlying the torus,

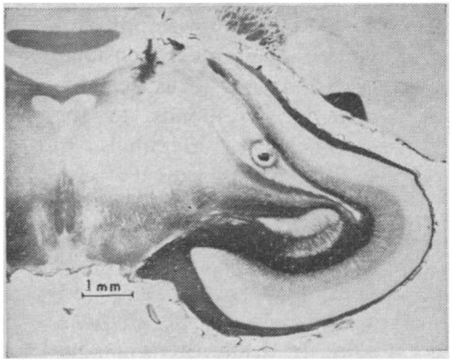

Fig. 1. Location of a low-threshold site from which alarm calls were evoked by stimulation at 30 μa. This site lies in the torus (biceps-shaped nucleus) and is marked by a small round lesion with a dot in the center (cross section of optic lobe of redwinged blackbird; fiber stain).

each of 66 points along five tracks in four birds yielded vocalization. Two sites in the medial part of the nucleus isthmi pars principalis parvicellularis of two birds were positive but had high thresholds (500 μa); the main body of this nucleus was not tested. Negative results were obtained from each of 16 tectal sites along seven tracks in five birds; from each of four sites along three tracks in the white matter ventral to the nucleus isthmi pars principalis parvicellularis in three birds; from five sites on one track within a millimeter of the midline at the level of the nucleus trochlearis; and from two sites in the ventromedial area of the tegmentum in two birds.

Vocalizations obtained from most points were tape-recorded (*14*). Typically, the calls were loud and rapidly uttered; near the threshold current, the rate of calling sometimes varied directly with strength of the current. Calls appeared immediately or after a latency of a few to many seconds, depending on current intensity; after a brief initial burst the rate of calling usually slowed. The vocalizations evoked by electrical stimulation at moderate intensities most closely resembled calls given at the approach of a potential predator or calls given by individuals being caught in their cages and held in the hand; these were mostly variants of the "tchuck" type of call (*15*). Often the calls resembled rapid "scolding." "Whistle type" calls (*15*) were not obtained from the midbrain, although in other experiments they were evoked from the hypothalamus.

Alarm calls have been obtained by electrical stimulation probably of the epistriatum (archistriatum) of parrots (*16*). Various types of calls have been evoked by electrical stimulation of the brains of chickens, but the responsive areas were not delineated anatomically (*17*) except in the hypothalamus, where androgen implants were used (*18*). In ducks, quacking has been evoked by electrical stimulation of the archistriatum (*19*) and mechanical stimulation of the tegmental midbrain (*20*), and mention has been made of squawks obtained by stimulation of the mesencephalon of the southern lapwing (*Belonopterus chilensis*) (*21*). An alarm call (*22*) and "Rückcuh" (*23*) or threat coo of feral pigeons (*Columba livia*), accompanied by the bowing display typical of the species, have also been obtained by stimulation of the brain (*24*).

My results show that the torus and the underlying gray matter are the most important midbrain areas for the control of alarm calls in redwinged blackbirds. Low thresholds were found as soon as the electrode entered the torus, and the lowest thresholds were consistently located in the belly of the torus and just beneath it. This finding is important for two reasons. (i) The torus has been considered to be an auditory way-station (*12, 25*), and in mammals, stimulation of the inferior colliculus that supposedly corresponds to the torus is not known to yield vocalizations. (ii) The torus is not a midline structure, as is the mammalian central gray matter.

The view that the torus is primarily an auditory sensory nucleus corresponding to the inferior colliculus of mammals rather than a motor integrative area is based on anatomical considerations, and there is anatomical, physiological, and behavioral evidence against this view. The torus appears to receive an input from the lateral lemniscus in the pigeon (*25*), but Craigie was unable to trace lateral lemniscus fibers into the torus in hummingbirds (*26*). That the torus may actually have little to do with audition was suggested by Erulkar's (*27*) failure to find evoked electrical responses to clicks in the torus while finding them in the adjacent "nucleus isthmi complex" known to receive fibers from the lateral lemniscus (*26, 27*). The physiological and behavioral experiments described indicate that the torus is not primarily an auditory structure.

Anatomically there are similarities between the central gray matter of mammals and the torus of other vertebrate classes. Both border the ventricle, both stand out as clearly delineated nuclear structures in the dorsal part of the brain stem, and both lie just inside the optic tectum. The difference in location is correlated with the lateral position of the optic tectum in birds and the medial position of the superior colliculi in mammals. In view of the correlated anatomical, physiological, and behavioral evidence, it seems reasonable to suggest that the central gray matter in mammals is the anatomical and functional counterpart of the torus of other vertebrate classes.

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