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Comparative Commissure Function: Interocular Transfer of Successive Visual Discriminations in Cats[1]

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FRANCIS, A., A. J. ELBERGER AND M. S. GAZZANIGA. *Comparative commissure function: Interocular transfer of successive visual discriminations in cats.* PHYSIOL. BEHAV. **28**(2) 295–299, 1982.—Intact and chiasm-sectioned cats were tested for interocular transfer after monocular training of a successive two-choice discrimination task. Similar tasks were previously employed to demonstrate complete failure of interocular transfer in both commissure-intact pigeons and goldfish. In contrast, both groups of cats showed clear interocular transfer. The results provide evidence for differing functional capacity in analogous interhemispheric pathways among vertebrates, and suggest that interocular transfer of successive visual discriminations may be a suitable paradigm for study of phyletic differences in behavioral ability.

Visual discrimination   Interocular transfer   Brain interhemispheric pathways   Cat

RECENTLY Green, Brecha and Gazzaniga [14] reported a puzzling failure of interocular transfer in pigeons tested on successive visual discrimination problems. In this task, as studied in a 3-key operant paradigm, the same stimulus (either colors or patterns) appearing on both side keys signalled a correct response to the right key, while a second stimulus appearing on both keys signalled a correct response to the left key. Interocular transfer was shown by pigeons in the same apparatus when identical stimuli were employed in a simple simultaneous discrimination. The failure of transfer could not be related to stimulus or response complexity per se, since the same stimuli and apparent response (peck left or peck right) were used in both situations. The failure of transfer was not related to problem difficulty, as judged by ease of learning, or by lack of prior experience with interocular transfer tasks, since experienced birds also failed to show transfer on successive discrimination tasks. In subsequent work, these findings in pigeons have been extended. A signal detection analysis, based on response latencies, confirmed the lack of stimulus discrimination; failure of transfer was also observed in successive discriminations based on luminous flux (Francis and Brecha, unpublished). Since these problems were easily learned in monocular training, the results suggest that interocular transfer of successive visual discriminations is difficult or apparently absent in pigeons.

These results can be distinguished from other reported failures of interocular transfer in birds and fish. For instance, in pigeons, Graves and Goodale [13] replicated Levine's [19, 20, 21] earlier findings of failure to obtain interocular transfer using a jumping response. Stevens and Klopfer [30] demonstrated that interocular transfer of an avoidance response depends on the particular aversive UCS employed in training. In these studies, failure of interocular transfer may depend on the use of specific stimuli or responses, since other workers have shown excellent interocular transfer in pigeons using simultaneous discriminations in free-operant paradigms [6, 13, 24]. Interocular transfer in fish may also depend on the discriminative stimuli employed [15,16] as well as the type of response [22].

Preliminary studies of successive discriminations in the cat and goldfish indicated that cats readily transferred while goldfish, like pigeons, failed to transfer. Green *et al.* [14] suggested that the organization of the central visual pathways in these various species may be a critical factor in interocular transfer. Unlike fish and birds, where the optic nerve is completely directed to the opposite hemisphere [7, 17, 28, 29], the cat has major direct visual connections to both hemispheres [18].

We now report that in cats, reliable interocular transfer occurs on a successive pattern discrimination problem when initial monocular training is directly accessible to only one hemisphere or to both hemispheres. This selective channel-

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ing of visual input to one or both hemispheres was achieved by comparing intact cats to those with midline section of the optic chiasm.

METHOD

Subjects

Six adult cats of both sexes were used: three were unoperated and three had previously undergone midline section of the optic chiasm by a transbuccal approach similar to that described by Myers [25,26]. The cats were housed in a communal cage and fed Purina cat chow. They were 23-hr food deprived before each daily session. All had prior experience in interocular transfer tests with simultaneous patterned stimuli in the present apparatus [10].

Apparatus

The cats were trained in a double two-choice training box. It consisted of two identical chambers (60×45×30 cm) separated by guillotine door. On each end were mounted two 10×10 cm stimulus panels which could swing out to allow access to a recessed food cup mounted in the floor behind each panel. These food cups were always filled with Gerber's beef baby food, which served as a reward. Above each of the stimulus panels was a two-Watt white bulb which was used for initial shaping. A 40-Watt house light was mounted in the ceiling of each chamber.

The stimuli were black patterns printed on white cardboard sheets which could be inserted onto the swinging panels. The stimulus pair (a bull's eye and six wheel spokes) was equated for flux, and each stimulus was mirror-symmetric. Opaque plastic occluders were inserted over one eye just before the daily session to effect monocular vision. Errors were judged by the visible and audible abutment of the cat's snout to the incorrect door as observed through a one-way observation window mounted in the ceiling of each chamber.

Procedure

The cats were previously trained in the apparatus and were proficient in performing monocularly. Forty trials per day were given with no corrections. Each trial consisted of the presentation of the same stimulus on both panels under an activated house light. One normal and two chiasm-sectioned cats were trained to push the right panel when both stimuli were "bull's-eye" and to push the left panel when both panels bore the "wheel spoke" stimulus. The other cats were trained on the opposite problem. At the end of the trial, the house light was extinguished, and the stimuli were manually arranged in the other chamber. The stimuli were always manipulated, even if no change was required, to prevent cueing. The house light in the adjacent chamber was then activated, and the guillotine door opened. The cats moved from the dark chamber to the illuminated chamber for the next trial. The order of the trials was determined by modified Gellerman sequences, in which there was a maximum of three successive trials with the same correct choice, and an equal total number of left and righ correct choices per session. All cats were trained with the right eye occluded. Training continued until a criterion of 36/40 (90%) was met for two successive days. Following criterion, the occluder was inserted in the left eye at the next daily session for transfer testing which continued at 40 trials per day until a criterion of 36/40 was met for two successive days. No corrections were allowed in training or transfer sessions.

TABLE 1

MEDIAN NUMBER OF DAYS TO COMPLETE CRITERION (RANGE)

	Training	Transfer
Chiasm-sectioned	14 (12–15)	6 (3–10)
Intact	15 (10–38)	3 (2–6)

Histology

Two to six months after completion of this study, the chiasm-sectioned cats were sacrificed by barbiturate overdose and perfused intracardially with saline followed by 10% Formalin. The brains were removed, embedded in Celloidin, and sectioned at 40 μ. Every tenth section was stained with cresyl violet and every eleventh section was stained by the method of Mahan. The optic nerves and tracts were examined as far posteriorly as their entrance to the thalamus. It was determined by light microscopy that no fibers crossing the midline existed. In additon, adjacent structures were examined, revealing no incidental damage as a result of chiasm section. Figure 1 shows a representative section stained by the method of Mahan. Ipsilateral optic tracts can be seen coursing to the thalamus, but a complete absence of fibers is seen at the midline (chiasm) region.

RESULTS

There was no significant difference between the intact and the chiasm-sectioned cats on number of days to reach either the training or the transfer criterion (Table 1, Mann-Whitney U, $p>0.1$). Therefore, the rates of learning and transfer were not affected by section of the optic chiasm.

In addition, both the intact and chiasm-sectioned cats demonstrated clear evidence of transfer, as shown by the significant improvement in the first two days transfer scores over the first two days training scores in both groups ($p<0.05$, Friedman tests). The results, expressed as the median percent correct scores, are shown in Fig. 2. Performance was at or near chance for both groups on the first two days of training since they typically showed a side preference.

DISCUSSION

The present study demonstrates interocular transfer of successive visual discriminations of patterned stimuli in intact cats and cats with retinal projections restricted to one hemisphere. Pigeons and goldfish show complete failure of transfer on similar tasks ([14] and unpublished observations). In searching for the essential characteristic which both distinguishes these vertebrates and may be related to the behavioral data, we believe it is worth considering the organization of the central visual pathways.

In both birds and fish, the major primary optic projections from the eye are almost completely directed to the opposite hemisphere, where the largest number of axons synapse in the optic tectum [7, 27, 28]. Interhemispheric communication proceeds via the supraoptic decussation, a structure which interconnects heterotopic visual areas [1, 2, 8, 17, 32].

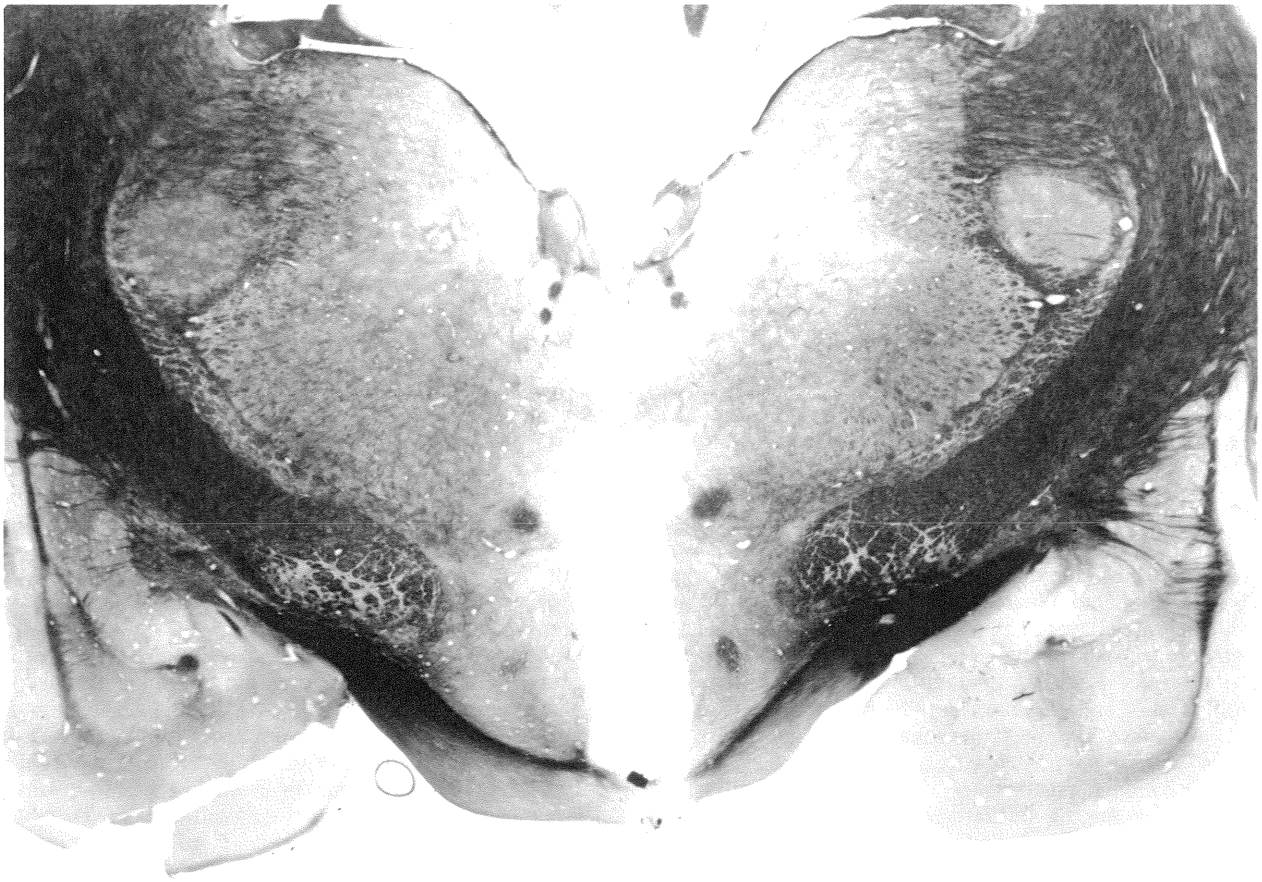

FIG. 1. Typical coronal section (40 μ) in the region of the optic chiasm, stained by the method of Mahan for myelin. The density of black color indicates the extent of myelination. Complete section of the chiasmal fibers is apparent, as is the resulting demyelination in the midline region.

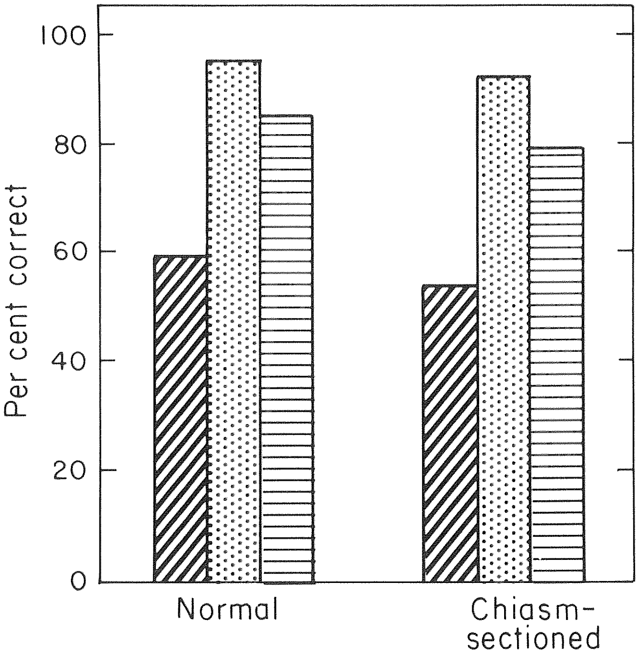

FIG. 2. Results showing median percent correct in both groups on the first two days of training (diagonal bars), last two days of training (at criterion, stippled), and first two days of transfer (horizontal bars).

The supraoptic decussation is heterotopic in that it interconnects different structures of the two hemispheres. It is one segment of a possible polysynaptic relay connecting corresponding forebrain visual areas in one hemisphere to those of the other. In mammals such as the cat, the organization is markedly different with fewer primary projections to the optic tectum as well as the presence of major direct projections from each eye to both hemispheres [18]. The comunication of interhemispheric visual information is mediated by the corpus callosum, a forebrain commissure with primarily homotopic connections between areas of the cerebral cortex [8,11]. The corpus callosum is homotopic in that it interconnects the same structures of the two hemispheres. Alternatively, if the corpus callosum is sectioned in primates or man, the remaining anterior commissure may subserve interhemispheric visual transfer [27,31].

Although the organization of both the primary and interhemispheric visual pathways differs among these species, we believe that the apparent behavioral distinctions can be best related to the latter. After section of the optic chiasm, the cat is similar to the intact goldfish and pigeon in that the remaining optic nerve fibers are directed only to one hemisphere, although in the cat it is to the ipsilateral hemisphere. Despite this anatomical similarity, the behavioral data suggest that the interhemispheric pathways in chiasm-sectioned cats (corpus callosum) can mediate transfer on the successive discrimination task, while it appears that the analogous pathways (supraoptic decussations) in goldfish and pigeon can not.

Previous work on the interhemispheric integration of visual learning in vertebrates [8, 9, 12] generally supported the concept that information obtained by one eye-hemisphere was accessible to the other eye-hemisphere via commissural pathways. The differing commissural pathways were considered functionally equivalent. In light of the present and prior data with the successive discrimination task, it appears that these analogous commissures are not equivalent in behavioral function.

The successive discrimination task requires retention over trials of stimulus information, since only one stimulus is presented on any given trial. In the simultaneous task both stimuli are presented at the same time on each trial. If the apparently greater mnestic and processing demand in successive discrimination tasks is coupled with potentially inefficient, poorly elaborated, or delayed transfer via polysynaptic, heterotopic interhemispheric pathways, transfer may fail. More efficient transfer might be expected when homotopic connections are employed. According to this view, vertebrates having heterotopic interhemispheric visual pathways (e.g., fish, birds) would be at the disadvantage in behavioral tasks requiring rapid interhemispheric processing and retention of stimulus information over trials.

An alternative hypothesis arises from possible selective attention and response biases during training. Under monocular viewing pigeons and fish (with laterally-placed eyes) may attend to the ipsailateral stimulus while cats (with frontally placed eyes) are able to view both stimuli. Differing behavioral strategies may result in these species. A cat viewing one stimulus on both doors may learn to go to the right and with a second stimulus to the left. The pigeon or fish may be making a stay/switch discrimination since it may not see both discriminanda: stay on this side if one stimulus; switch to the other side if the other stimulus. In testing for transfer with the other eye open the pigeon would have to reverse the direction (relative to the non-viewing eye) of response to each stimulus, creating potential conflict. For example, if the stimulus red signals a choice to the right, with the right eye open the pigeon learns to go to the side of the open eye. With the left eye open in a transfer test, the pigeon must now choose the side away from the open eye. This conflict could account for the failure of interocular transfer in animals using this strategy.

Analysis of the errors made by pigeons does not support this interpretation of the failure in transfer. Green *et al.* [14] found that the errors made by the pigeons in the successive discrimination transfer task, as in initial training, derive from side preferences. The birds performed at or near chance, rather than reversing the correct behavioral strategy, which would have produced scores much less than 50% correct. In addition, studies with other tasks have shown that split-chiasm cats and pigeons differ in the ability to interocularly transfer lateral mirror-image discriminations [3]. In this situation split-chiasm monkeys perform as do intact pigeons rather than split-chiasm cats [3]. These issues could be clarified in studies of successive visual discrimination tasks which employed vertically-arrayed discriminanda, eliminating the left-right response requirement, as well as the study of birds with frontally-placed eyes and mammals with laterally-placed eyes.

Taken together, our data on species differences with the successive task argues for phyletic variation in behavioral capacity. Previous work has shown differences in behavioral capacity among mammals, birds, and fish [4,5]. As a model paradigm the interocular transfer of successive visual discriminations reveals a clear distinction between pigeons and fish compared to cats. The critical variable may be whether the pathways mediating interhemispheric transfer interconnect heterotopic or homotopic brain regions. The behavioral distinction across species on this task seems more robust than prior work on phyletic differences [4,5], and we suggest that this paradigm can be exploited for further studies in comparative psychology. This paradigm would be particularly useful for psychobiological purposes as well, since the probable brain structures involved, the interhemispheric pathways, are identified.

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