

Role of Visual Cortex in Interocular Transfer in the Cat

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Received August 6, 1970

The role of the visual cortex (areas 17, 18, and 19), with its preponderance of binocular cells, was investigated as a locus important for interocular transfer. Fourteen cats were tested for interocular transfer of a series of brightness and pattern discriminations in a two-choice, positive reinforcement paradigm. Three were controls. Eleven underwent manipulations designed to reduce the number of binocular cells in their visual cortices. The manipulations were: rearing with external strabismus induced by neonatal transection of one or both medial rectus muscles and/or surgery in adulthood to cut midbrain and forebrain commissures (but not the optic chiasm); and ablation of areas of visual cortex. Measurements of immediate transfer and relearning scores evaluated interocular transfer. Controls showed complete transfer of every discrimination, which contrasts to transfer failures of some tests seen with every experimental cat; three cats reared with strabismus and no adult surgery and three normally reared cats with adult brain lesions showed transfer deficits. These results suggest a role in interocular transfer for the binocular cells of the visual cortex. Two different methods to reduce their number resulted in transfer deficits. This implies that few binocular cells in the visual cortex can subserve good interocular transfer, or the geniculocortical regions outside of areas 17, 18, or 19 can subserve interocular transfer.

Introduction

One of the problems facing students of the mammalian central nervous system is the relationship of behavior to neural features as measured by the test tube, microscope, and oscilloscope. One approach to this problem is to relate gross changes in the brain (usually by surgical ablation) to resultant changes in behavior. There are, however, alternate methods of obtaining neural changes. Animals reared in certain abnormal environ-

¹ This research was aided by USPHS Grant 2-TO1-GM00281-11 and was carried out as partial fulfillment for a Ph.D. degree. The author expresses gratitude to Drs. J. M. Sprague and E. Stellar for their helpful advice and to the Australian National University, Physiology Department of Professor P. O. Bishop, for assistance in preparation of the manuscript. The author's present address is Physiology Department, Australian National University, Canberra City, A.C.T. 2601, Australia.

ments (such as sensory deprivation) have brains sufficiently different from their normally reared counterparts to be discriminated by various means (15). My purpose was to define visual behavior in cats with their visual systems altered by specific visual deprivation or surgery, or both.

In the deprivation studies, the medial rectus muscle of one eye was transected 8–10 days after birth. The resultant external strabismus deprived these cats of normal binocular vision. Hubel and Wiesel (5, 6) carried out electrophysiological studies on such cats, as well as normally reared animals, and found that over four-fifths of the cortical cells of normal cats are binocular; that is, they can be driven by appropriate photic stimulation of either retina. In cats reared with strabismus, Hubel and Wiesel reported that both retinæ drive cortical cells, but less than one-fifth of these units display binocularity despite normal responses by other criteria. Therefore, the most striking physiological consequence of strabismic rearing in cats is a marked diminution of binocular interaction on the cells of the striate cortex.

Reduction of binocular interaction has also been attempted by one or both of the following surgical procedures: removal of areas of visual cortex to reduce the number of binocular cells; and extensive commissurotomy, including the corpus callosum, hippocampal commissure, anterior commissure, posterior commissure, habenular commissure and the commissure of the superior colliculus (but not the optic chiasm) to prevent the convergence which occurs across the midline. Several investigators have reported such convergence through the corpus callosum which presumably enhances the binocular interaction of cells in the visual cortex (2, 7).

Such a large reduction in binocularly activated cells in the cat's visual cortex, whether achieved through strabismic rearing, surgery, or both, would be expected to produce behavioral consequences, any of a number of which could have been chosen for study. The one emphasized in this report was a reduction in interocular transfer. Normal cats routinely demonstrate interocular transfer; that is, upon monocular learning of a visual task (such as a pattern discrimination) the cat responds with the naive eye to subsequent monocular testing as if that eye had been exposed during initial learning. This requires some form of binocular interaction in at least one site between optic nerve input and behavioral output. For several reasons the cat's visual cortex seems a likely site for at least part of this interocular transfer process: The learning of pattern and brightness discriminations normally seems to take place in the cat's cortex (1, 10, 17, 20); the visual cortex, with its preponderance of binocular neurons, provides a necessary locus of binocular integration; and the classical split-brain preparation, produced by transection of the optic chiasm and forebrain commissures, which has poor interocular transfer (12, 18, 19), was found to have only monocular neurons in the visual cortex (2). Therefore, previous work had

already implicated the cat's visual cortex as important to the learning and transfer phenomena studied in the present experiments.

Materials and Methods

Eleven adult cats of both sexes were tested for interocular transfer in this experiment. Ten were laboratory born and reared, and one cat (C3ReA) was introduced into the laboratory as an adult. Table 1 provides a list of all of these cats including the experimental manipulation prior to testing.²

TABLE 1
DESCRIPTION OF CATS PRIOR TO TESTING^a

Cat no.	Sex	Procedure prior to testing
C1	F	Normal control
C2	M	Normal control
C3ReA	F	Control. MR of right eye cut in adulthood
C4S	M	Section of CC, HiC, AC, PC, HaC and SCC in adulthood
Le1	F	MR of left eye cut at 9 days of age
Re2	M	MR of right eye cut at 10 days of age
Re3	M	MR of right eye cut at 10 days of age
Re4S	F	MR of right eye cut at 10 days of age, section of CC, HiC, AC, PC, HaC and SCC in adulthood
C1SV	F	Section of CC, HiC, AC, PC, HaC, and SCC, plus large bilateral lesion to visual cortex in adulthood
C5V	M	Small bilateral lesion of visual cortex in adulthood
Le1SV	F	Same as Le1 plus section of CC, HiC, AC, PC, HaC and SCC, with a large bilateral lesion of visual cortex in adulthood
Re4SV	F	Same as Re4S plus a large bilateral lesion of visual cortex following commissurotomies in adulthood
Be5V	M	MR of right eye cut at 8 days of age, MR of left eye cut at 23 days of age, a small bilateral lesion of visual cortex in adulthood
Be6SV	M	MR of right eye cut at 8 days of age, MR of left eye cut at 23 days of age, a large bilateral lesion of visual cortex in adulthood.

^a Abbreviations: MR, medial rectus; CC, corpus callosum; HiC, hippocampal commissure; AC, anterior commissure; PC, posterior commissure; HaC, habenular commissure; SCC, commissure of the superior colliculus.

Surgical Procedures. Section of one medial rectus was performed on six kittens at 8–10 days of age, two kittens at 23–24 days of age, and one adult cat (C3ReA) by a method modified from the description of Hubel and Wiesel (6). All brain surgery was performed under routine aseptic condi-

² Table 1 has 14 entries because three cats were tested before and after various experimental manipulations. Thus the same individuals are C1 and C1SV, Le1 and Le1SV, Re4S and Re4SV.

tions and, as noted in Table 1, was performed on adult cats. Pentobarbital sodium (35 mg/kg body wt, ip) was the anesthetic, and atropine sulfate (0.6 mg, sc) was given to reduce salivation. A bone flap was removed (and replaced after surgery), the duramater was retracted, and cortical lesions were produced by gentle subpial suction. Midsagittal sectioning of all commissures (except that of the superior colliculus) was performed by a method adapted from that of Myers (12). For that of the colliculus, a fine knife was inserted along the midline under the tentorium, and this last commissure was cut to an approximate depth of 2 mm.³ Brain surgery was performed on one stage in all cats except Re4SV, which had the cortical ablation 9 months after the commissurotomies.

Only adult cats (i.e., at least 8 months of age) were tested in these experiments. Cats with medial rectus section in infancy had, of course, several months intervention between surgery and testing. A 1–4 week postoperative period intervened before cats which had any surgery in adulthood were tested.

Apparatus. Cats received interocular transfer testing by means of food approach motivation in a two-choice apparatus similar to that described by Sechzer (16). This consisted of a runway with two exit doors and a short barrier extending into the runway from between the doors. Each door carried a stimulus plaque, and this stimulus-door assembly was switched from side to side in a Gellermann sequence (4).

The stimulus plaques were translucent Plexiglas rectangles as shown in Fig. 1. The light–dark stimulus pair (Fig. 1a) were two plain, translucent rectangles: “light” was transilluminated and “dark” was not, producing a brightness ratio between them of 25:1. All patterned stimuli, created with black, opaque tape (Fig. 1b–d), were transilluminated from behind; and each pair was equilibrated for area of pattern and for brightness.

Interocular Transfer Testing Procedure. During all testing, visual input was restricted to one eye by means of a rubber mask (11). Cats were placed on a feeding schedule, receiving nearly all of their food (small pieces of beef spleen) during testing; supplementary food was given on weekends and other nontest days. All cats were shaped to the test paradigm before discrimination testing. They learned to navigate the runway and to exit by pushing through an unlocked door for food, switching rapidly from locked to unlocked door. The doors were of transilluminated plain Plexiglas (light in Fig. 1a); the locks were switched in a Gellermann sequence (4). All cats were then tested on the same initial discrimination: light vs. dark with dark positive.

³ Occasionally cats have tentoriums so far forward as to preclude collicular commissurotomy by this approach, but none was encountered in this series.

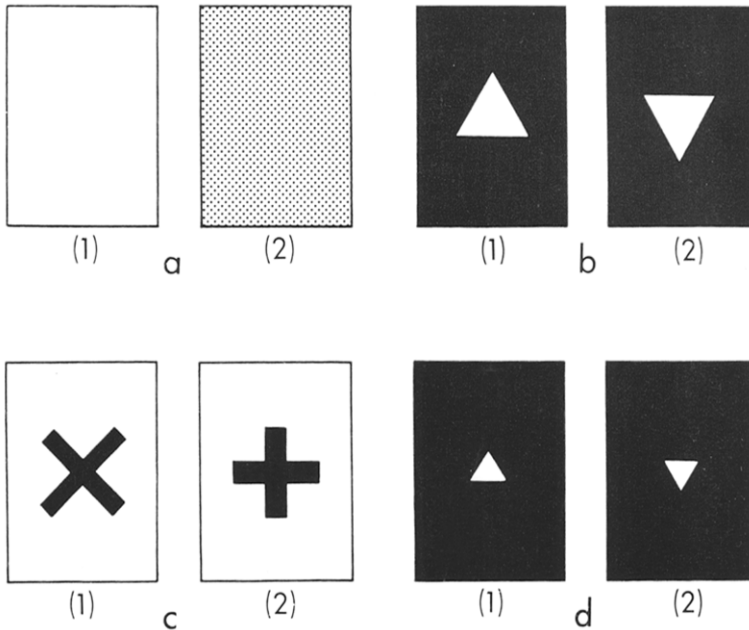


FIG. 1. Stimulus pairs for discrimination testing. a. Translucent Plexiglas transilluminated for "light" and not transilluminated for "dark." b-d. Transilluminated Plexiglas with black, opaque tape arranged to create patterns as shown; these are equilibrated for area of pattern and brightness. The number (1) or (2) identifies each stimulus of a pair and is used in Tables 2 and 3 to indicate the positive stimulus of each pair.

The following procedure was used during testing for every discrimination. An error was recorded if the cat pushed against the locked door with the negative stimulus after which the cat could push through the correct, unlocked door on the other side of the barrier. A cat ran 40 trials a day monocularly using only the first eye (eye A) until reaching a criterion of four or less errors a day for 2 consecutive days. On the next day (the transfer day) eye A was tested during the first 20 trials, then another monocular mask was fitted to occlude eye A and expose the naive eye (eye B) for the day's final 20 trials. One transfer score (T) was computed from this data by comparing the initial experiences of eyes A and B to each other and to the 90% criterion level by the formula :

$$T = \frac{\% \text{ correct first 20 trials eye B} - \% \text{ correct first 20 trials eye A}}{90\% - \% \text{ correct first 20 trials eye A}} \times 100,$$

The first 20 trials of eye B refer to the transfer day whereas those of eye A refer to the initial exposure of the cat to the discrimination. Thus the formula expresses transfer as the improvement of eye B's initial responses

due to the experiences of eye A. Following the transfer day, each cat was then tested with eye B until reaching the aforementioned criterion level. A second transfer score, or savings (S), is computed from:

$$S = \frac{\text{number of trials to criterion eye B}}{\text{number of trials to criterion eye A}} \times 100,$$

(Trials at or above criterion are not included in this computation.) This expression describes transfer as the improvement of eye B's learning rate due to eye A's experience.

An attempt was made by the following method to ensure that the correct stimulus of a discrimination pair would not have been naturally preferred by the cat without the positive-reinforced learning procedure. Before this learning procedure the cat ran 11 trials with both stimulus doors of a discrimination pair unlocked and randomly switched from side to side. Whichever stimulus was chosen five or less times became the correct one during the subsequent learning trials. This procedure was followed for every cat with every discrimination.

Anatomical Procedures. Following completion of their testing schedules, all operated cats were killed under sodium pentobarbital anesthesia and gravity perfused with normal saline solution followed by 10% formalin-saline solution. Eyes which had the medial rectus muscle cut were carefully dissected to reveal the pattern of extraocular musculature remaining. Brains containing lesions were blocked on a stereotaxic apparatus, removed, embedded in 12% celluloidin, coronally sectioned in 40- μ slices, and every 10th and 11th section was stained by Mahon and Nissl techniques. These were studied to map the extent of neural ablations. Commissurotomies were evaluated simply and effectively using the Mahon sections. The degree of retrograde degeneration in the dorsal lateral geniculate bodies, using the maps of Garey and Powell (3), supplemented direct observations of cortical cell and fiber patterns to assess the extent of cortical extirpation.

Results

All cats before discrimination testing were able to perform simple visually guided tasks with either eye and involving either visual hemifield. These tasks included visual placing and object following. Cats with large lesions (Le1SV, Re4SV, Be6SV, and C1SV) produced sluggish and inconsistent responses. All cats with sectioned medial rectus muscles possessed a clear external strabismus when compared to the normal cats. This strabismus varied considerably between animals, and the estimated range of strabismic angles was 15°–45°. Strabismic cats were seen during binocular following responses to fix with only one eye. Unlike Hubel and Wiesel's report (6), alternate fixation (one eye, then the other) was never seen. The fixating

eye always was the eye with intact muscles or, in the cases of Be6SV and Be5V, the second eye which had the medial rectus cut. This fixating eye is referred to as the nonstrabismic eye; the other, the strabismic eye.

Dissection of the orbits of all strabismic cats revealed no medial rectus fibers remaining intact after these muscles had been sectioned. Nor were there any obvious anatomical differences (scars, etc.) among these eyes that might explain the strabismic variability seen.

Histological reconstruction of the lesions showed a few isolated surviving fibers in the commissure of the superior colliculi, representing less than 5% of the intact commissure, in three cats (C4S, Le1SV, and Re4SV). None survived in cats C1SV or Be6SV. In all five cats, no fibers remained in the corpus callosum or the posterior, habenular, hippocampal, or anterior commissures. The extent of cortical extirpation is summarized in Fig. 2. The smallest lesions (C5V, Be5V) removed a considerable but undetermined number of binocular cells. The largest lesions (C1SV, Le1SV, and Re4SV) removed virtually all of areas 17, 18, and 19, as described by Otuska and Hassler (14), and invaded parts of the suprasylvian gyri as well. The large lesion in cat Be6SV spared many binocular cells of area 17, but completely removed areas 18 and 19.

Monocular Learning. A summary of this initial learning with eye A is given in Table 2, which shows for each cat the discrimination learned, the positive stimulus (+), whether eye A was strabismic (S) or nonstrabismic (N), and the number of trials to criterion for eye A. Comparison between groups shows no significant difference between learning scores, but this may reflect heterogeneity. When only those cats with cortical ablations were compared with the controls, no difference was seen in scores for the light-dark discriminations, but controls required fewer trials to learn the small triangles (the only pattern discrimination on which all cats were tested) than did cats with cortical ablation ($p < .05$ on a t -test). Table 2 also shows that scores achieved with strabismic eyes were not strikingly different from those achieved with nonstrabismic eyes.

No explanation is offered for the surprising performance of cat Re2 on solving the large-triangle discrimination. After three errors in the first five trials, only one further error was made; criterion was, therefore, achieved immediately and maintained during subsequent testing with eye A.

Interocular Transfer. Table 3 presents a summary of the interocular transfer data. It shows for each cat the discrimination tested, the positive stimulus (+), and the transfer (T) and savings (S) values. No control cat showed the slightest transfer deficit, whereas every experimental cat had some deficit ($p < .001$ on a t -test). Because of the lack of homogeneity of the experimentals, it is difficult to say which specific procedures could produce a transfer deficit. However, within the experimental group, three

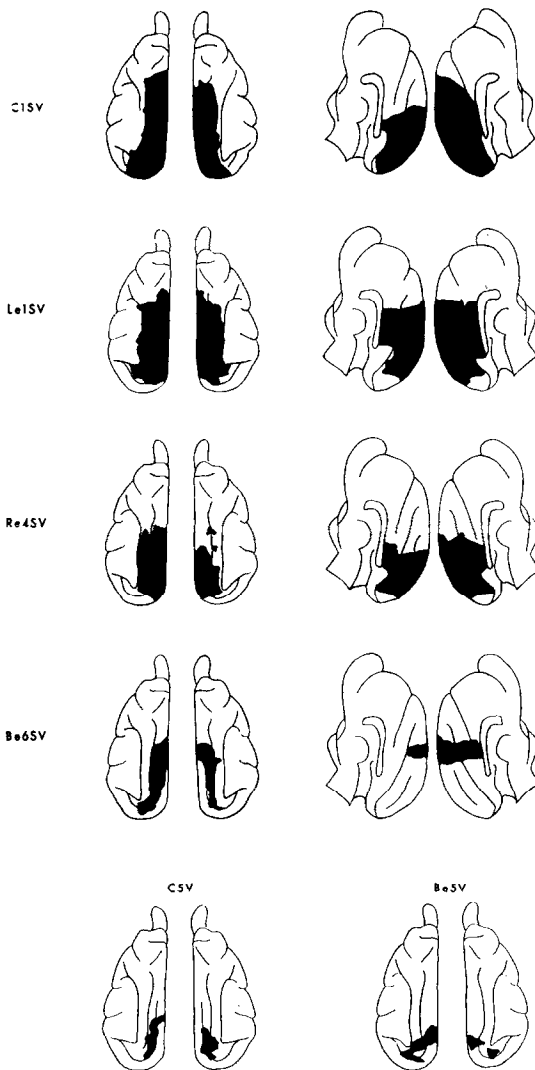


FIG. 2. Summary of cortical lesions as reconstructed from serial stained sections of cortex and thalamus. Lesion areas shown in black.

cats reared with strabismus and no subsequent adult surgery (Le1, Re2, and Re3) and three normally reared cats with adult brain lesions (C1SV, C4S, and C5V) showed transfer deficits ($p < .05$ and $p < .02$, respectively, on t -tests of T or S scores). Thus either experimental manipulation by itself interfered with interocular transfer.

The transfer deficits were equally large for the light-dark discriminations and for the pattern discriminations. The T and S scores, which yielded two

TABLE 2
RESULTS OF MONOCULAR LEARNING^a

Cat no. ^b	Pair a		Pair a		Pair b		Pair c		Pair d	
	+	A NTC	+	A NTC	+	A NTC	+	A NTC	+	A NTC
C1	2	N 240	1	N 280	1	N 40			2	N 720
C2	2	N 240	1	N 120			1	N 200	1	N 640
C3ReA	2	S 160	1	N 160			1	S 240	1	N 800
C4S	2	N 240	1	N 120	2	N 680			1	N 720
Le1	2	S 240	1	N 280	1	S 80			2	N 720
Re2	2	N 160	1	S 120	1	S 0			2	N 720
Re3	2	N 160	1	S 160	1	N 280			2	S 1240
Re4S	2	N 120	1	N 80	1	S 160			2	S 680
C1SV	2	N 80							2	N 1920
C5V	2	N 80	1	N 160	2	N 320			1	N 680
Le1SV	2	S 120	1	N 80			1	N 200	1	S 1360
Re4SV	2	S 200	1	N 120			1	S 200	1	N 960
Be5V	2	S 200	1	N 200	1	N 440			2	S 1040
Be6SV	2	N 200	1	S 240	1	S 440			2	N 1240

^a With a reference to Fig. 1, the discrimination pairs (a-d) and positive stimulus for each pair (1 or 2 in column "+") can be ascertained. Also shown is whether eye A was normal (N) or strabismic (S) in column "A" and the number of trials to criterion (NTC).

^b Cats C1, C2, and C3ReA are controls.

TABLE 3
RESULTS OF INTEROCULAR TRANSFER SHOWING FOR EACH TEST
THE T AND S SCORES^a

Cat no. ^b	Pair a		Pair a		Pair b		Pair c		Pair d	
	+	T S	+	T S	+	T S	+	T S	+	T S
C1	2	100 100	1	100 100	1	100 100			2	100 100
C2	2	100 100	1	100 100			1	100 100	1	100 100
C3ReA	2	100 100	1	100 100			1	100 100	1	100 100
C4S	2	50 75	1	71 83	2	92 97			1	100 100
Le1	2	100 100	1	53 64	1	33 25			2	100 100
Re2	2	100 100	1	100 100	1	0 0			2	100 100
Re3	2	100 100	1	72 91	1	100 100			2	100 100
Re4S	2	50 83	1	100 100	1	100 100			2	43 97
C1SV	2	90 75							2	56 52
C5V	2	49 75	1	100 100	2	100 100			1	57 97
Le1SV	2	89 16	1	76 0			1	90 90	1	17 69
Re4SV	2	100 100	1	71 83			1	100 100	1	40 93
Be5V	2	100 100	1	94 90	1	100 100			2	77 78
Be6SV	2	100 100	1	67 92	1	80 86			2	50 95

^a The discrimination pairs and positive stimulus for each pair are designated as in Table 2.

^b Cats C1, C2, and C3ReA are controls.

different measures for the interocular transfer phenomenon, were not significantly different from each other ($P > .20$ on a t -test) and had a significant positive correlation ($r = +0.58$, $P < .001$). This implies that immediate transfer and savings are closely related processes, if not parts of a single process. Finally, a significant negative correlation ($r = -0.65$, $P < .01$) existed between number of trials to criterion of eye A and interocular transfer (either T or S scores) for cats tested on the small triangles (the only pattern discrimination with sufficient data points for statistical analysis). No such correlation was seen between learning and transfer of the light-dark discriminations. This indicates that failures to transfer discriminations are related to difficulty in learning them if they are patterned, but not if they are light-dark.

Discussion

Two major points are drawn from this work. First, cats with strabismic rearing, commissurotomy, and/or visual cortex lesions are measurably deficient in interocular transfer of learned discriminations. Cats with only strabismic rearing or adult brain lesions suffer deficiency in such transfer. Careful study of the interrelationships of transfer and learning scores provide useful insights into the nature of these phenomena.

Interocular Transfer Deficits. The results show that cats with experimentally reduced binocular interaction of single cells suffered a partial deficit in interocular transfer. Three features characterize this finding. First, cats with very few functional cells left in areas 17, 18, and 19 (Le1SV, C1SV, Re4SV, and Be6SV) did surprisingly well in their learning and transfer tasks, suggesting the importance of the anatomically defined visual areas outside 17, 18, and 19. For instance, other recent studies in the cat have shown a large visual input to such cortex from the lateral geniculate nucleus (8, 13) and from the superior colliculus via the posterior nucleus or pulvinar (13). In the second place, different experimental techniques (strabismus vs. brain surgery; commissurotomy vs. cortical ablation; etc.) did not produce correlative differences in the transfer deficit measurable by the present methods. Thirdly, a single experimental cat demonstrated great variability in its transfer scores on a series of tests. These scores often fluctuated unpredictably between perfect and very poor transfer irrespective of the discrimination. Taking the average over-all deficit as approximately a 20% failure, it seems more appropriate to characterize this as a 20% probability of a relatively large failure (regardless of the type of discrimination) and an 80% probability of little or no failure, rather than to say such a cat is likely to show a 20% failure on all tests. In other words, when a cat has part of its transfer potential interrupted its transfer behavior becomes unpredictable. This contrasts both to normal cats with full

transfer potential and reliably complete transfer of all discriminations and to cats with optic chiasm and midline commissures severed with little transfer potential and predictably poor transfer of any test (9, 12, 18, 19). Any explanation of the interocular transfer phenomenon, then, must take this variability into account.

Significance of Statistical Correlations Among T, S, and Learning Scores. Statistical analysis of the present data sheds some light on the mechanisms underlying interocular transfer. The particular advantage of the present data for such analysis is that it includes as data points nearly the entire spectrum of transfer from virtually none to perfect. Past experiments, chiefly with split-brain preparations, had only the two ends of the transfer spectrum to study. The correlations between both *T* and *S* scores as well as transfer and learning is more enlightening when thus studied.

Previous investigators studying interocular transfer have used immediate transfer scores (similar to the *T* scores in this experiment) and relearning scores (*S* scores). Despite the coupling of perfect transfer with complete savings and transfer failure, with no savings, it has never been shown that these are measures of the same process. The significant correlation of and lack of difference between a wide range of *T* and *S* scores shown here do suggest they are two measurements of either the same process or closely related processes. This finding is consistent with the following mechanism. The process of monocular learning establishes a memory trace, a fraction of which is available to binocular cells and the remainder to monocular cells activated only by the "exposed" eye. If this binocular fraction is sufficiently high, a sufficiently complete memory trace is available to the "naive" eye such that when the cat is tested with that eye it shows perfect interocular transfer (perfect *T* and *S* scores). If this fraction is very low, virtually no trace is available to the second eye and the cat shows no interocular transfer (zero *T* and *S* scores). Finally, for intermediate fractions, a partial trace is available to the cat through the second eye which leads to partial interocular transfer (partial *T* and *S* scores), the extent of which is related to the size of the aforementioned binocular fraction of the memory trace created through the exposed eye.

The correlations between transfer and learning are puzzling. On the one hand, the negative correlation seen on the pattern discriminations has been previously described in split-brain cats (16) and can be explained in both cases by the same process. Namely, each eye recruits fewer cortical cells as a consequence of fewer binocular neurons, which both prolongs learning and reduces transfer. This is true for all gradations of transfer, not just the end points of perfect or nonexistent transfer. On the other hand, no such correlation is seen between learning and transfer of light-dark discrimina-

tions, despite the report of such a negative correlation in split-brain cats which fail to transfer brightness discriminations (9).

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