dial forebrain bundle is in reasonable agreement with the experimental findings available regarding the time course of degeneration in central nervous system fibers. It is possible, therefore, that both the chemical and behavioral changes are related in some fashion to the effects of progressive nerve degeneration in areas of the brain lying outside the primary locus of the lesion.

It is not clear whether the close correspondence between these changes in brain serotonin and jump threshold reflects some functional role for serotonin in determining the sensitivity of an animal to electric shock. It is interesting, however, that lesions placed in the septal area of the rat have also been reported to produce significant decreases in serotonin concentration of the brain (*6*) and an increased sensitivity to electric shock (*9*).

It is well established that a denervated or decentralized smooth muscle (for example, iris or nictitating membrane) is more sensitive to the effects of medullary catecholamines released by painful or stressful stimuli (*8*). Further, the development of such a supersensitivity in a smooth muscle has been demonstrated to follow a time course which approximates the time required for the progressive degeneration of the severed nerve. The development of an increased sensitivity to painful stimuli following lesions in the medial forebrain bundle is strikingly analogous to those effects of peripheral nerve section. If we use the terminology of Cannon and Rosenbleuth (*8*) a lesion in the medial forebrain bundle may prove to be a "central denervation" and the resultant increased sensitivity to electric shock may represent a "central denervation supersensitivity."

Regardless of the interpretation of these findings it is clear that the effects of some central nervous system lesions on behavior cannot be interpreted categorically but must be defined with respect to the time after surgery. Further investigations of the progressive anatomical or neurochemical changes induced by a lesion in the remaining portions of the brain may help to clarify the nature of such time-dependent phenomena.

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Interhemispheric Reversal of Mirror-Image Oblique Lines after Monocular Training in Pigeons

Abstract. *Pigeons, with one eye open, were reinforced for pecking at a 45° oblique line (/). When the opposite, untrained, eye alone was open, pigeons responded maximally to the mirror-image (135° \) of the training stimulus (45° /). This unexpected interocular reversal of mirror-image stimuli has not been reported for any other species.*

In the visual system of the pigeon, the primary afferent input from each eye projects to the contralateral optic tectum. Both anatomical (*1*) and physiological (*2*) data indicate that there is complete crossing of the optic nerve fibers at the optic chiasma. However, visual information presented to only one eye must reach the ipsilateral half of the brain because pigeons trained monocularly on color, brightness, and certain form discriminations can perform the same task using the untrained eye (*2–4*).

The functional capacity of the interhemispheric integrating systems has been examined in a variety of species. Many investigators have studied the extent of transfer of a monocularly trained discrimination as it is affected by difficulty (*5*); degree of transformation of the test stimulus (*6*); or as a function of the visual dimension (that is, color, form, brightness) primarily involved (*7*). Since patterns which are mirror-image pairs provide the same amount of visual information, they are a convenient vehicle for studying interhemispheric transfer as a function of alterations in the shape and number of elements of the discriminative stimuli. In this report, two experiments are described, each concerned with the interhemispheric transfer of mirror-image oblique lines which can be distinguished only by their angular orientation. Pigeons are able to discriminate oblique lines, although this discrimination has proved more difficult for octopuses, fish, and children (*8*) to learn than a discrimination of horizontal versus vertical lines.

In the first experiment, generalization along a continuum of angular orientation was examined in pigeons after they were given monocular training on a single angle. Once an organism has been reinforced for responding to a particular stimulus (S+), it also responds to other stimuli which share properties in common with S+. Response rate decreases as a function of the distance of these stimuli from S+ along a particular continuum and thereby indicates which stimuli an organism regards as "similar" to a given stimulus (S+) associated with reinforcement. Several investigators (*9*) have found that pigeons will generalize along a continuum of angular orientation after binocular training, but there have been no studies of interhemispheric transfer of generalization following monocular training.

Five experimentally naive, male Carneau pigeons were trained to peck a translucent key, 25 mm in diameter, mounted on a vertical panel. A 45° line, 3 mm in width and 25 mm in length, was projected on the key from a miniature display unit. The box was dark except for the discriminative stimulus during training and testing sessions. All the pigeons wore brass goggles (*2*) which permitted restriction of visual stimulation to one eye during training sessions. The pigeons were maintained at 75 to 80 percent of their "free feeding" weight.

The pigeons were trained in a standard operant conditioning apparatus and schedules of reinforcement were programmed with transistor circuitry. Each training session terminated when the pigeon had been reinforced with food 60 times. A variable interval schedule (*10*) was used during training, so that performance would be minimally disrupted during the generalization tests which were run without reinforcement. Only the first peck made after a variable interval of time resulted in access to grain for 6 seconds. To ensure a steady rate of response during generalization tests, the pigeons were trained for 25 sessions during which the mean of the variable interval was gradually increased until it equalled 4 minutes. Pigeons were given five daily training sessions on a variable interval of 30 seconds, six sessions on a variable interval of 1 minute, and six on a variable interval of 3 minutes; finally they were maintained on a variable interval of 4 minutes for 8 days before generalization testing was begun.

Generalization tests consisted of six presentations, lasting 30 seconds, of each of 12 angles of tilt going by 15° steps from 0° to 165°. These 12 tilts were presented, without an intertrial interval, in a different random sequence during each generalization test. On each of 3 days, each pigeon was given a generalization test first with the trained eye open and then with the untrained eye open—a total of six generalization tests for each pigeon. Each day of generalization tests was preceded by five reinforcements given on a variable interval schedule of 3 minutes with the trained eye alone open, and after completion of both generalization tests each pigeon earned 50 reinforcements on a variable interval schedule of 4 minutes.

The generalization gradient obtained with the trained eye open is shown on the left of Fig. 1. The total number of responses for each pigeon was averaged over 3 days and a relative generalization gradient (on the ordinate) was computed by assigning a value of 1.00 to total responses to the 45° stimulus associated with reinforcement during training. Responses to other degrees of tilt are expressed as decimal portions of this value. The generalization gradient obtained with the untrained eye open is shown on the right of Fig. 1. It was necessary to assign the value of 1.00 to the 45° line since this was the stimulus trained as positive in the opposite eye. Each curve is based on the responses of four pigeons since the fifth pigeon failed to respond during tests with the untrained eye and could not be included. Therefore, each point in each gradient is based upon responses to 72 presentations of that particular tilt.

With the trained eye alone open, all pigeons responded maximally to the 45° line, the stimulus present during training, and gave progressively fewer responses to stimuli dissimilar from the 45° line. However, with the untrained eye alone open, all pigeons responded maximally to a 135° line, the mirror-image of the line present during training (45°). The maximum of the generalization gradient obtained with the untrained eye open was shifted by 90° from the maximum of the gradient obtained with the trained eye open. Statistical analysis of each gradient showed that the difference between the number of responses to the 45° and the 135° lines was significant (Mann-Whitney U test, one-tailed; $p < .014$ for the trained eye, $p < .029$ for the untrained eye).

These data indicate that, in the course of interhemispheric transfer, the 135° line was taken as the equivalent of its mirror-image, the 45° line present during training. This unexpected left-right inversion is especially puzzling since the pigeons saw only the 45° line during training. However, one cannot conclude that the pigeon's visual world is seen in conflicting ways with opposite eyes, but merely that the untrained eye does not "recognize" the training stimulus, 45°.

Table 1. Responses during extinction tests obtained from pigeons trained monocularly to discriminate a reinforcement-associated stimulus ($S+$) from a stimulus ($S-$) never associated with reinforcement for responding.

Pigeon	Trained eye open		Untrained eye open		Training sessions (No.)
	$S+$	$S-$	$S+$	$S-$	
	Discrimination of striped oblique lines				
A	663	19	22	51	12
B	471	8	4	39	12
C	712	5	0	52	12
	Discrimination of two parallel oblique lines				
D	193	0	5	107	12
E	590	0	0	62	20
F	1390	40	686	1009	40
G	607	13	61	36	20
	Discrimination of single oblique lines				
H	455	8	30	212	16
I	3550	85	101	551	20

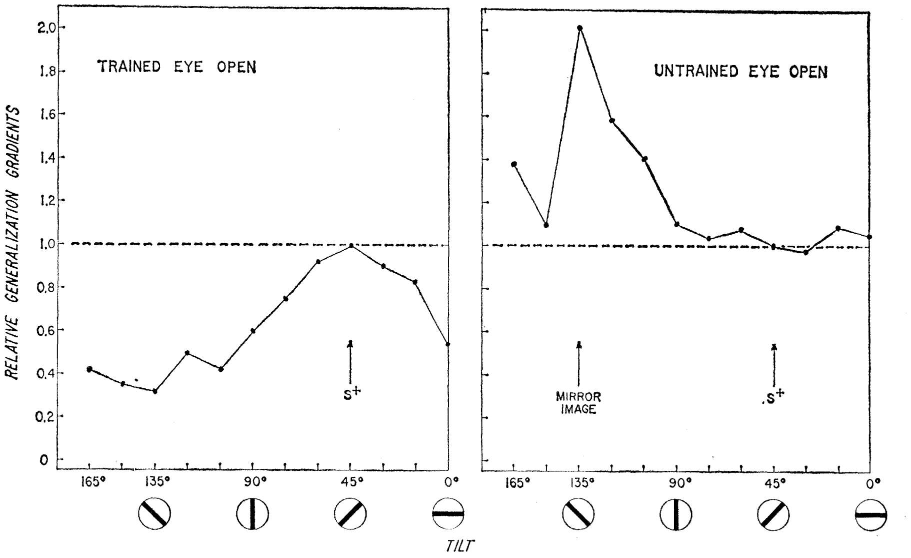

Fig. 1. Relative generalization gradients on a continuum of angular orientation obtained from pigeons that were trained monocularly to peck at a 45° oblique line for food reinforcement.

It is important to examine those possible explanations of this reversal phenomenon which are amenable to behavioral analysis. For instance, if a pigeon tilts its head toward the eye viewing the discriminative stimulus, then a 45° line on the left retina and a 135° line on the right retina would be "similar" in that each would approach the horizontal axis of the head. Careful observation showed that all pigeons pecked with their heads held in an upright position, interspersed with many rapid movements to both the left and right. As another alternative, it might be argued that if a pigeon with its left eye open pecks at the center of an oblique line slanting toward the midline (45°) the upper portion of the line may be obscured by the beak and only the lower portion may be visible. Whereas, if the oblique line slants away from the midline (135°) only the upper portion may be visible. When the same stimuli are presented to the opposite eye, these relationships are exactly reversed. This possibility could be minimized by making the oblique lines reduplicated throughout the entire field.

In the second experiment, three subjects from the first experiment were trained to discriminate a striped pattern of 45° oblique lines (S+) from a striped pattern of 135° oblique lines (S−). Four other pigeons were trained on a monocular discrimination of two parallel oblique lines, and two pigeons on a discrimination of single oblique lines also oriented at 45° (S+) and 135° (S−). When the positive stimulus (S+) was present, pecking was reinforced at variable intervals averaging 1 minute. Five-minute presentations of S+ alternated with presentations of the negative stimulus (S−) during which no reinforcements were available. The duration of S− was determined by the pigeon's behavior; that is, termination of S− and return to S+ was contingent upon at least 1 minute of no pecking. Any peck during the presentation of S− reset a clock and lengthened the time that S− was present. This combination of reinforcement schedules produces a high rate of response during S+ and a low or zero rate during S−. Tests consisted of ten 2-minute presentations of S+ and S− in a single alternation sequence, first to the trained eye, then to the untrained eye. No reinforcements were available during test sessions.

As shown in Table 1, all pigeons learned the discrimination with the trained eye open, but eight out of nine responded maximally to S−, the mirror-image of S+ during tests of interhemispheric transfer with the untrained eye open. These results strengthen the conclusion of the first experiment and make it unlikely that the mirror-image reversal observed was a function of the movement of the pigeon's beak in the visual field.

Interhemispheric reversal of a visual mirror-image discrimination has not been reported for another species. There are no anatomical or electrophysiological data available on pigeons which would predict interocular reversal of forms distinguishable only by left-right orientation. A point-to-point representation of the visual field of one eye on the contralateral optic tectum has been found in the pigeon (*11*), but there is no evidence concerning the pattern of tectal-tectal projections, and the pathways subserving interhemispheric transfer of color and pattern information are as yet undetermined (*2*).

The only published evidence on another species with completely crossed optic-nerve fibers suggests that there is a spatial equivalence in the mapping of left-right relations in the visual field on the optic tecta. An electrophysiological analysis of the projection of the binocular field on the frog optic tecta (*12*) showed that corresponding retinal points project to the same point on one optic tectum. However, it may be that the ipsilateral projections are not concerned with interhemispheric transfer since (i) transection of the intertectal and posterior commissures does not abolish the ipsilateral tectal response to monocular stimulation in frog (*13*), and (ii) fish, which have no ipsilateral tectal representation of monocular input (*14*), show interocular transfer of form and color discriminations (*15*).

There are behavioral data showing that the portion of the retina stimulated is critical to interocular transfer in pigeons under certain training conditions (*4*). It is important to note that visual stimulation was not restricted to a specific portion of the retina in either of the present experiments. It is apparent that a 135° line should maximally stimulate the upper temporal and lower nasal quadrants of the left retina and the upper nasal and lower temporal quadrants of the right retina. If only those areas receiving input from corresponding portions of the retina are directly connected between the optic tecta, then an interocular reversal of oblique lines would be less paradoxical.

These behavioral data showing interhemispheric reversal of left-right mirror-image lines encourage an examination of how visual space is ordered from optic tectum to optic tectum in pigeons. There are several observations which suggest the capacity of each hemisphere to function independently with respect to visual stimulation. Pigeons do not have conjugate eye movements and are usually described as using a single eye at a time, even though there is a 24° binocular field (*16*). Further, pigeons are able to learn a successive conflicting discrimination in each eye (*3*). A capacity to dissociate conflicting visual inputs might permit adaptive visual function, despite an inequivalence of visual-spatial mapping from optic tectum to optic tectum.

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