*INTEROCULAR GENERALIZATION: A STUDY OF
MIRROR-IMAGE REVERSAL FOLLOWING
MONOCULAR DISCRIMINATION
TRAINING IN THE PIGEON¹*

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Generalization gradients along a continuum of angular orientation were obtained from four pigeons, following monocular training on a discrimination between a 45° oblique line (S+) and a 135° oblique line (S-). All pigeons were trained on a chain DRO VI 1 schedule of reinforcement. Generalization gradients obtained with the trained and untrained eye were compared. All pigeons responded maximally to the 45° line (S+) when tested with only the trained eye open. During generalization tests of interocular transfer with only the untrained eye open, three pigeons responded maximally to S- (135°), the mirror-image of the stimulus associated with reinforcement during training (45°). The other pigeon failed to show interocular transfer of the discrimination. Interocular reversal of left-right mirror-image stimuli has not been reported for any other species.

The anatomy of the pigeon visual system differs from that of mammals in that the optic pathways are completely crossed (Cowan, Adamson, and Powell, 1962; Mello, Ervin, and Cobb, 1963) and each optic tectum receives direct information only from the contralateral eye. Despite this lateralization of visual input, pigeons monocularly trained to discriminate colors or certain patterns can perform the same task while using the untrained eye (Levine, 1945; Mello *et al.*, 1963; Catania, 1965). For example, if pigeons with only one eye open are reinforced for responding to a cross but not a circle, tests with only the untrained eye open show continued control of responding by the discriminative stimuli. Since discriminative stimuli which are, by definition, novel to the untrained eye, nevertheless control the pattern of responding when only the untrained eye is open, visual information must have been relayed from one brain half to the opposite side of the brain.

Interocular transfer has been demonstrated in a variety of species in which the visual input is restricted to one side of the brain either anatomically (Menkhaus, 1957; Muntz, 1961; Sperry and Clark, 1949; Schulte, 1957) or surgically (Myers, 1953; Downer, 1962). Fail-

ure of interocular transfer may be attributable to the difficulty of the discrimination (Ingle, 1963; Myers and Sperry, 1958) or to the degree of transformation of the stimulus (Schulte, 1957). However, in each instance where interocular transfer occurred, it has been veridical with respect to the discriminative stimuli used during training. The subject has responded appropriately to the stimuli trained as positive and negative during transfer tests with its untrained eye.

In one instance of non-veridical interocular transfer after monocular training (Mello, 1965a), it was found that monocularly trained pigeons reinforced for pecking at a 45° oblique line (S+) responded maximally to its mirror image (135°) during generalization tests with the opposite untrained eye open. There are no anatomical or electrophysiological data available on pigeons which would predict interocular reversal of left-right mirror-image patterns and this phenomenon has not been reported for any other species.

The original observation of interocular reversal of a mirror-image pattern during generalization tests was obtained without differential reinforcement of 45° and 135° (Mello, 1965a). The present study examined the consistency of the mirror-image reversal phenomenon by analyzing generalization gradients obtained with each eye in turn, following monocular discrimination training. It was anticipated that generalization testing would prove to be a sensitive method for de-

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termining the limits of the mirror-image reversal phenomenon, since it involves successive comparison of several stimuli along a continuum of orientation. Tests of transfer involving only the two stimuli used during discrimination training cannot show the extent to which the reversal phenomena extends to other stimuli along the same continuum. If pigeons do have the capacity to show veridical interocular transfer of left-right mirror-image patterns, then a generalization testing procedure might show, for example, a peak at both S— and S+. There have been no previous studies of interocular generalization involving multiple stimuli, following monocular discrimination training (*cf.* Muntz, 1962).

METHOD

Subjects

Four male White Carneaux pigeons wore brass goggles (Mello *et al.*, 1963) which permitted stimuli to be presented to only one eye during training and testing sessions. The goggles obscured the lateral visual field and restricted vision to the anterior visual field. Each pigeon was maintained at between 75 and 80% of its free-feeding weight during the experiment.

Each pigeon had been monocularly trained to discriminate mirror-image patterned circles (Mello, 1965*b*). The S+ was a circle bisected by a vertical line; the left half of the circle contained vertical stripes and the right half contained horizontal stripes. The S— was identical to S+ except that the left-right position of the vertical and horizontal stripes was reversed. The same eye of each pigeon was trained to minimize the possibility that the previous discrimination training might affect the shape of the generalization gradients obtained with the untrained eye.

Apparatus

The experimental chamber was a clear Plexiglas box (12 by 12 by 14 in.) enclosed in an outer chamber of plywood lined with Styrofoam. An aluminum panel containing apertures for the response key (25 mm in diameter) and the grain feeder (2 by 2¼ in.) was attached to one end of the experimental chamber. The response key, grain feeder, and projection equipment were located outside the

experimental enclosure. No house lights were present in the box.

Stimuli were projected on a single response key from a modified one-plane-digital-display unit supplied by Industrial Electronic Engineers, Inc. The discriminative stimuli were oblique lines (25 mm by 3 mm) oriented respectively at a 45° angle (S+) and a 135° angle (S—). Schedules of reinforcement were programmed by transistor circuitry in an adjoining room. The experimental chamber was well ventilated and a white masking noise was present at all times.

Training and Testing Procedures

Four pigeons were monocularly trained to discriminate a 45° oblique line (S+) from a 135° oblique line (S—) on a chain DRO VI 1 schedule of reinforcement (Ferster and Skinner, 1957; Reynolds, 1961). During S+, the first peck made after a variable interval of time averaging 1 min resulted in access to grain for 6 sec. 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 min of no pecking in the final schedule. The DRO requirement of no response was gradually lengthened from 5 sec to 1 min according to the following daily progression: 5, 10, 15, 20, 20, 30, 30 sec and 1 min. This procedure was used in an attempt to maximize the stability of the discrimination before tests of interocular transfer by minimizing the opportunity for errors. This procedure was suggested by Terrace's (1963) observation that chlorpromazine failed to disrupt performance of pigeons trained on an "errorless fading procedure" as compared to control pigeons trained with errors. The procedure followed in the present experiment departed from Terrace's in that new values of S— were introduced only at the beginning of a session, rather than within a single session. Each session ended after 60 reinforcements and each pigeon was trained for 18 sessions before generalization testing began.

Generalization tests consisted of 12 presentations of each of six angles of tilt, ranging between 0° and 165° in 30° steps. These six stimuli were presented for 30-sec periods, without an intertrial interval, in the following

sequence: 45°, 135°, 15°, 75°, 135°, 45°, 105°, 15°, 165°, 105°, 75°, 165°. This sequence was repeated six times during each generalization test. No reinforcements were available during generalization testing.

A persistent problem in interocular transfer experiments is the tendency of pigeons to respond at a low rate when tested with the untrained eye alone. In order to increase overall response rates during generalization tests of

Fig. 1. Cumulative records of typical patterns of responding during monocular discrimination training on a chain DRO VI 1 schedule of reinforcement. For each pigeon, the upper trace shows cumulative responses as a function of time. Each discrete downward deflection of the pen indicates the occurrence of a food reinforcement. Each downward deflection of the pen that coincides with an upward deflection of the baseline pen indicates a change of the discriminative stimulus from S+ to S-. The lower trace indicates the schedule of reinforcement in effect: where the pen is depressed, the stimulus was a 45° oblique line and responses were intermittently reinforced; where the pen is elevated, the stimulus was a 135° oblique line and responses were not reinforced.

interocular transfer, each pigeon with its untrained eye open, pecked at a white key on a VI 1 min schedule on the day preceding the final training session. This white key session terminated after 60 reinforcements. Each generalization test was preceded by a 10 reinforcement warm-up session on a white key. Reinforcements were programmed on a VI 30 sec schedule during each warm-up. Each pigeon was tested, first with its untrained eye alone open, then with its trained eye open, on each of three successive days.

RESULTS

Cumulative records of the final performance of each pigeon on a chain DRO VI 1 schedule of reinforcement are shown in Fig. 1. Differential stimulus control over rate of responding was clearly established for each pigeon. During the last five days of discrimination training, the number of responses during S— accounted for less than 6% of the total responses in each session for three pigeons. The other pigeon's (N91) responses during S— accounted for 12% of its total responses in one session.

Figure 2 shows that all pigeons responded maximally to S+ (45°) during generalization tests with the trained eye open. However, when only the opposite, untrained eye was open three pigeons responded maximally to S— (135°), the mirror-image of S+ (45°). Pigeon N85 failed to show interocular transfer of the discrimination. Relative generalization gradients were computed by averaging the total number of responses to each tilt for each pigeon over the three tests, and assigning a value of 1.00 to that orientation to which animals responded most frequently. Responses to other degrees of tilt are expressed as a decimal fraction of this value.

Comparison of the generalization gradients of each pigeon with its trained and its untrained eye open in turn, shows that gradients obtained during tests of interocular transfer are not mirror-images of gradients obtained with the trained eye open. Only the performance of N91 approaches a point-for-point mirror-image equivalence if responses to 15°, 45°, and 75° obtained with its trained eye open, are each compared with responses to 165°, 135°, and 105° respectively, obtained with its untrained eye open. However, each

pigeon showing interocular transfer of the discrimination responded to S— as if it were the equivalent of S+, and N92 and N89 also responded to S+ as if it were the equivalent of S—.

DISCUSSION

The capacity of various species to discriminate between oblique lines has been a point of considerable controversy since Sutherland's (1957a) observation that octopuses have more difficulty discriminating between two oblique lines than a horizontal versus a vertical line. Sutherland (1957b, 1960) has discussed the implications of these data for a theory of pattern perception. Comparable data indicating the relative difficulty of an oblique line discrimination problem have been obtained on fish (Mackintosh and Sutherland, 1963), rats (Lashley, 1938), and children (Rudel and Teuber, 1963). Although it is agreed that cats can discriminate between oblique rectangles, Parriss (1964) has concluded that oblique lines are more difficult to discriminate than horizontal versus vertical rectangles whereas Sutherland (1963) found these problems were of comparable difficulty. The method of training was similar in each experiment, but Sutherland (1963) compared two groups of cats, whereas Parriss (1964) trained each cat on each problem, using appropriate controls for effects of the sequence of training.

In pigeon, several investigators (Honig, Boneau, Burstein, and Pennypacker, 1963; Hearst, Koresko, and Poppen, 1964) have observed sharp generalization gradients on a continuum of angular orientation after reinforcement of responding to a horizontal or to a vertical line. Zeigler (1965) has found that pigeons can discriminate between oblique lines in both a simultaneous and a successive discrimination situation. In the present experiment, there is little question that each pigeon learned to discriminate between oblique lines (Fig. 1) and responded appropriately to these discriminative stimuli when other tilted lines were also presented (Fig. 2, left). These data, which show interocular reversal of left-right mirror-image oblique lines (Fig. 2, right), cannot in any way be interpreted in terms of difficulty in discriminating oblique lines during training.

Fig. 2. Relative generalization gradients on a continuum of angular orientation obtained from pigeons monocularly trained to discriminate a 45° oblique line (S+) from a 135° oblique line (S-).

Clearly, interocular transfer of information occurred in each pigeon that showed the reversal phenomena. The precision of the degree of interocular transfer achieved is dramatized by the fact that the peak of the generalization gradients occurred at S- (135°), the mirror-image of S+ (45°). Given that information concerning angular orientation can be transferred interocularly, the non-veridical transfer of left-right mirror image patterns is all the more puzzling. There are no anatomical or physiological data which would predict interocular reversal of left-right mirror images (cf. Mello, 1965a). The effective stimulus dimension which provides the basis of similarity between opposing mirror-image forms during interocular transfer is unknown.

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