INTEROCULAR TRANSFER OF DISCRIMINATIONS IN THE PIGEON¹

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Pigeons with one eye covered were trained to discriminate intensities or colors of stimuli located to one side of the head, or intensities, colors or forms of stimuli located in front of the beak. Each discrimination transferred to the covered eye, even when previous training with the covered eye included the reversal of the tested discrimination. Pigeons also were able to learn conditional discriminations in which appropriate responding depended on which eye was covered.

Levine (1945a, 1945b, 1952) has reported that only discriminations of stimuli located in certain parts of the visual field transfer from one eye of the pigeon to the other. In his experiments, most of which used a Lashley jumping stand modified for pigeons, Levine distinguished between anterostral and subrostral stimuli: anterostral stimuli were located¹ in front of the bird, slightly below its line of sight; subrostral stimuli were located below the bird's head. Discriminations of subrostral stimuli transferred from one eye to the other, but discriminations of anterostral stimuli did not. Also, anterostral-subrostral transfer did not take place even within a single eye.

The present experiments observed a distinction between anterior stimuli, located in front of the beak, and lateral stimuli, located to one side of the bird's head. This distinction, different from Levine's, followed naturally from operant techniques with pigeons, in which the bird pecks at a key in front of its beak (e.g., Ferster and Skinner, 1957), and was consistent with the apparent anterior near-sightedness and lateral far-sightedness of the pigeon (Catania, 1964). The relationship between this distinction and Levine's distinction

between anterostral and subrostral fields is discussed below.

In the present experiments, each pigeon was trained with one eye covered to peck a key in the presence of one stimulus but not in the presence of a second stimulus that alternated with the first. Later, the pigeon's ability to respond appropriately to the stimuli with the previously covered eye was tested. In one procedure, the discrimination tested for transfer to the covered eye was the reversal of a discrimination learned earlier with that eye. This procedure provided the pigeon with a history of responding to the stimuli with each eye, and therefore made it unlikely that tests of interocular transfer would be affected by the novelty of the first presentation of a stimulus to a given eye or by differences in the pigeon's ability to peck the key with one or with the other eye covered.

METHOD

Subjects

Eight adult, male pigeons (two White Carneaux and six White Homers), experimentally naive at the beginning of these experiments, were maintained at about 80% of their free-feeding body weights. Over each eye of each pigeon, a goggle was mounted with flexible collodion to restrict the pigeon's field of view. One type of goggle restricted vision to the anterior field; a second restricted it to the lateral field and eliminated binocular viewing (cf. Catania, 1963). Either type could be capped, which served to limit vision to a single eye.

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Apparatus

Two experimental chambers were enclosed in sound-attenuating boxes and wired to appropriate programming and recording apparatus in a separate room. The general characteristics of the chambers have been described by Ferster and Skinner (1957).

One chamber was used to study discriminations of diffuse lateral stimuli. A grain feeder and a translucent response key, $\frac{3}{4}$ in. in diameter, were mounted on the main panel. A white 6 w lamp behind the response key provided general illumination. The houselights, in a translucent box mounted near the ceiling on the wall opposite the main panel, provided diffuse illumination: red and green 6 w Christmas-tree lamps were lit alternately for color discrimination, and two white 6 w lamps were turned on or off for intensity discrimination.

The second chamber was used to study discriminations of localized anterior and lateral stimuli. The main panel was modified so that stimuli could be presented either directly on the translucent key, $\frac{3}{4}$ in. in diameter (anterior stimuli), or on translucent screens, 1 in. in diameter, located on either side of the key (lateral stimuli). The lateral screens were about 4.5 in. apart, facing each other at an oblique angle (*cf.* Catania, 1963). Stimuli were projected on the key or on the lateral screens by Industrial Electronics Engineers' "One-plane Digital Display Units." Stimuli included red and green lights, a white light about 20 db brighter than the unilluminated screen, horizontal and vertical bars ($\frac{1}{8}$ by $\frac{5}{8}$ in.), a cross ($\frac{1}{8}$ by $\frac{5}{8}$ in. horizontal and vertical arms), and an open circle ($\frac{1}{2}$ in. outside and $\frac{1}{4}$ in. inside diameters). Figures were white on a dark background.

In both chambers, the grain feeder was located directly below the key, the feeder was lit and all other lights were turned off during reinforcement, and each operation of the key produced a feedback click from an ac relay.

Procedure

Preliminary Training. Through reinforcement of successive approximations to key pecking, each pigeon was trained to peck a key transilluminated with white light. After pecking was established, it was maintained by a variable-interval schedule of reinforcement (VI) the value of which was gradually ex-

tended until the interval between the end of one reinforcement and the availability of the next was, on the average, 3 min (*cf.* Ferster and Skinner, 1957). Goggles were then mounted, and training was continued until each pigeon was able to maintain VI performance with either eye covered. Pigeons with goggles limiting vision to the lateral field required extensive retraining after the goggles were mounted, because they could see neither the key while pecking nor the feeder while eating. For these birds, reinforcement duration was 10 sec. For birds with goggles limiting vision to the anterior field, reinforcement duration was 4 sec.

Discrimination Training. During training sessions, one eye of the pigeon was covered and a multiple schedule of reinforcement arranged VI reinforcement in the presence of one stimulus alternating with extinction (EXT) in the presence of a second stimulus. Training on a given discrimination consisted of at least seven daily sessions. In the terminal discriminative performance, the rate of pecking maintained by the 3-min VI schedule in the presence of the first stimulus alternated with a near-zero rate of pecking in the presence of the second stimulus.

For the pigeons tested with localized lateral or anterior stimuli, two successive 1-hr sessions were programmed for each pigeon on each day. One eye was covered during the first hour and the other eye during the second hour. The eye covered during the first hour was varied from day to day. While a given discrimination was programmed for one eye, training with the second eye consisted of either a different discrimination from that for the first eye or of maintained VI reinforcement in the presence of only the VI stimulus for the first eye. Multiple-schedule components lasted 2 min.

Discrimination training with diffuse lateral stimuli differed in several details: 4 min of the VI stimulus alternated with 2 min of the EXT stimulus in the multiple schedule; sessions were 6-hr long or longer; and only one session was programmed each day.

Transfer Procedures. Table 1 illustrates procedures used to test interocular transfer, with stimuli for a color discrimination used as an example. The first procedure, simple transfer, is illustrated by the initial discrimination training for the left eye followed by the exposure of the right eye to the multiple

Table 1

Illustration of procedures, with color discriminations as an example. The VI stimulus is indicated by (+) and the EXT stimulus by (-).

<i>Procedure</i>	<i>Left eye</i>	<i>Right eye</i>
Discrimination training	green (+) red (-)	covered*
Simple transfer test	covered	green (+) red (-)
Discrimination reversal	covered	green (-) red (+)
Reversal transfer test	green (-) red (+)	covered
"Conflict" (conditional discrimination)	[green (-) red (+) covered	covered green (+) red (-)]

*An alternative procedure is the programming of green (+) alone in separate sessions for the right eye.

schedule with the left eye covered. In a subsequent procedure, the reversal of the discrimination is trained with the left eye still covered, and, when the reversal is well-established, the right eye is then covered and the performance with the left eye is tested. In this procedure, the pigeon will respond according to the reversal, learned recently with the opposite eye, if interocular transfer occurs. But it will respond according to the original discrimination, learned earlier with the tested eye, if there is no interocular transfer. By arranging a discrimination for a given eye different from that whose transfer to that eye will be tested, this reversal transfer procedure: (1) controls for possible effects of stimulus novelty and of prior stimulus preference, (2) assures that the pigeon can attend to the locus of the discriminative stimuli and can respond with either eye covered, and (3) makes it possible to test the transfer of a given discrimination in a given pigeon more than once.

In the final procedure illustrated in Table 1—"conflict" or conditional discrimination—ap-

propriate responding is determined by which eye is covered. The original discrimination is programmed for the right eye, and the reversal of this discrimination for the left eye. These conditions are repeated from day to day in the alternate sessions for each eye. In the example, the performance appropriate to the conditional discrimination is responding to red but not to green when the left eye is uncovered, and to green but not to red when the right eye is uncovered.

Table 2 summarizes the tests performed with each type of discrimination. In each dark-light discrimination, the VI schedule was programmed during dark for the test of simple transfer, because each pigeon had originally been trained to peck on a lit key. In all other cases in which more than one pigeon was tested for the simple transfer of a given discrimination, at least one pigeon was tested with the multiple-schedule stimuli in reverse order (*e.g.*, red-green instead of green-red).

Some pigeons were tested with more than one discrimination, in sequences that varied

Table 2

Tests of interocular transfer. Except in the two cases noted, each entry represents the number of pigeons tested under the given condition.

<i>Stimuli</i>	<i>Location</i>	<i>Simple Transfer</i>	<i>Reversal Transfer</i>	<i>"Conflict"</i>
Dark-Light (diffuse)	Lateral	1		
Green-Red (diffuse)	Lateral	1	1	1
Green-Red	Lateral	2		
Dark-Light	Anterior	2	1	
Green-Red	Anterior	4	5*	1
Circle-Cross	Anterior	1		
Horizontal-Vertical	Anterior	4	6**	2

*Includes one pigeon tested twice.

**Includes two pigeons tested twice.

from bird to bird (*e.g.*, the sequence for Pigeon 234, shown below in Fig. 2, 3, and 4). In each case in which a simple transfer test for a given pigeon was preceded by tests of transfer with other discriminations, however, the simple transfer test was later followed by a reversal transfer test. The "conflict" procedure was programmed, for the four pigeons tested in this procedure, only after the transfer tests had been completed.

RESULTS

Interocular transfer of discriminations in the pigeon was demonstrated with each of the

transfer tests listed in Table 2. The conflict procedure indicated that pigeons can master a conditional discrimination in which appropriate responding depends on which eye is covered.

Simple transfer of a diffuse lateral color discrimination is illustrated in Fig. 1. The multiple schedule was programmed for the right eye (A). In alternate sessions with the left eye (B), VI reinforcement was programmed in the presence of green (+), the VI stimulus of the multiple schedule. Transfer was tested (C) by programming the multiple schedule for the left eye, with which the pigeon had never before seen red (-), the EXT stimulus of the

PIGEON 41: Lateral stimuli, VI3 and mult VI3-EXT

Fig. 1. Test of interocular transfer of a color discrimination (diffuse lateral stimuli) in Pigeon 41. The cumulative recordings show multiple schedule performance with the right eye (A), maintained VI performance in the presence of the VI stimulus of the multiple schedule with the left eye (B), and the first programming of the multiple schedule for the left eye (C). Prior to (C), Pigeon 41 had never seen the EXT stimulus with its left eye. Pips on the record during the VI stimulus, green (+), represent reinforcements; the recording pen was displaced downward during the EXT stimulus, red (-).

multiple schedule. A few pecks occurred during the initial presentations of red, but the overall performance was essentially the same as that maintained with the right eye.

A more complex sequence of transfer procedures is illustrated in Fig. 2, 3, and 4, the complete series of tests with Pigeon 234. The first two records in Fig. 2 show simple transfer of an intensity discrimination from the right eye to the left eye. Some pecking to light occurred during the first few presentations of this stimulus on Day 8, but the performance soon became appropriate to the multiple schedule. The discrimination was then reversed for the left eye (Day 9). The gradual emergence of a performance appropriate to the reversal is evidence of the completeness of the transfer of the original discrimination. During Day 9, the pigeon emitted many more pecks in the presence of the former VI stimulus, dark (-), than in the presence of the former EXT stimulus, light (+), despite the fact that no pecks were reinforced during the former stimulus and many pecks were reinforced during the latter. This performance

implies that reinforcement itself had not acquired a discriminative function, and that the performance on Day 8 was a genuine example of interocular transfer rather than of rapid learning with the left eye.

Within two weeks, the discrimination reversal was well-established (Day 21): maintained VI responding during light (+) alternated with a near-zero rate of responding during dark (-). The reversal was then programmed for the right eye (Day 22), and the pigeon responded according to the reversal, learned with the other eye, and not according to the original discrimination, previously learned with the tested eye. The pigeon emitted fewer responses to the EXT stimulus (-) in the reversal transfer test (Day 22) than in the simple transfer test (Day 8) possibly because the light and dark stimuli were not novel stimuli to the tested eye in the reversal transfer test. Another difference, however, is that the simple transfer test was programmed during the first session of Day 8, whereas the reversal transfer test was programmed during the second session of Day 22. Throughout

PIGEON 234: Anterior stimuli, mult VI 3-EXT

Fig. 2. Simple transfer and reversal transfer of an anterior intensity discrimination in Pigeon 234. The cumulative records show full sessions on the days indicated by the circled numbers: performance on the initial discrimination (Day 7); test of transfer of the discrimination to the left eye (Day 8); subsequent reversal of this discrimination (Day 9); terminal performance on the reversal (Day 21); and test of transfer of the reversal to the right eye (Day 22). Pips on the records, during the VI stimulus (+), represent reinforcements. The recording pen was displaced downward during and reset to the baseline at the end of each EXT stimulus (-).

these experiments, pigeons tended to emit more responses to EXT stimuli (—) in the first than in the second session on a given day.

Transfer tests of a color discrimination are shown in Fig. 3. These sessions were programmed alternately with those in Fig. 2 and 4; the day numbers correspond to those in the other figures. A green (+) red (—) discrimination in the left eye (Day 7) was followed by a test of simple transfer to the right eye (Day 8). The performance with the right eye was essentially the same as that with the left eye on the preceding day, demonstrating interocular transfer of the color discrimination.

The discrimination was maintained in the right eye for two weeks (Day 21). The absence of an effect of the concurrent reversal of the intensity discrimination in the left eye (Day 9, Fig. 2) on the performance with the right eye demonstrated that the color discrimination was not based on a difference in the intensities of the red and green stimuli.

In the sequence illustrated in Fig. 3, the reversal procedure was slightly modified. The discrimination reversal was programmed for the left eye (Day 22), the eye for which the original color discrimination (Day 7) had been programmed. For almost the full hour on Day 22, during which few reinforcements occurred, the performance appropriate to the original discrimination was maintained. Within two weeks, the discrimination reversal was well-established (Day 35), and transfer of this reversal to the right eye was tested (Day 36). Some pecking to green (—) occurred early during both Days 35 and 36, but the performance on the transfer test was appropriate to the reversal, learned with the left eye, rather than to the original discrimination, the only color discrimination previously programmed for the right eye (Days 8 through 21). If there had been little or no interocular transfer, the pigeon would have responded according to the last learned discrimination in the right eye,

PIGEON 234: Anterior stimuli, mult VI 3-EXT

Fig. 3. Simple transfer and reversal transfer of an anterior color discrimination in Pigeon 234. The records show performance on the initial discrimination (Day 7), test of transfer of the discrimination to the right eye (Day 8), maintained performance on the discrimination (Day 21), subsequent reversal of this discrimination in the left eye (Day 22), terminal performance on the reversal (Day 35), and test of transfer of the reversal to the right eye (Day 36). Details as in Fig. 2.

rather than according to the more recently learned discrimination in the opposite eye.

Figure 4 shows a sequence of procedures involving discrimination of horizontal and vertical bars. Again, the day numbers correspond to those in Fig. 3. The initial discrimination of horizontal (+) and vertical (−) with the right eye (Day 35) was followed by a test of simple transfer to the left eye (Day 36). Transfer occurred: the performances were essentially the same with each eye.

Subsequently, the conflict or conditional discrimination procedure was programmed: during the left-eye session each day, the original discrimination was maintained; during the right-eye session, this discrimination was reversed. On the first day of this procedure (Day 37), the pigeon responded according to the original discrimination with both eyes. After 12 days, the pigeon responded appropriately to the respective discriminations for each eye (Day 48). It emitted more pecks to vertical (+) than to horizontal (−) when the right eye was open, and more to horizontal (+) than to vertical (−) when the left eye was open. The

discriminative performance was sometimes not as accurate as some of the preceding performances (*e.g.*, Day 48, right-eye session), but the difference in the rates of responding to the two stimuli was maintained even in the absence of reinforcement, as during the first three presentations of the horizontal and vertical stimuli to the right eye on Day 48. Thus, the interocular transfer demonstrated in the preceding tests did not preclude successful performance in the conflict procedure. The pigeon was able to respond appropriately to a discrimination and to its reversal, when appropriate responding was determined by which eye the pigeon was using.

With differences in detail, such as the order in which the transfer of various discriminations was tested in different pigeons, results similar to those in the figures were obtained for the other discriminations listed in Table 2. There was no evidence of interactions between discriminations when a different discrimination was programmed for each eye. In addition, the fact that pigeons maintained the performances appropriate to a given discrimi-

Fig. 4. Simple transfer and "conflict" performance in Pigeon 234, with discrimination of anterior horizontal and vertical stimuli. The records show performance on the initial discrimination (Day 35), test of transfer of the discrimination (Day 36), first session of the "conflict" procedure (Day 37), and terminal performance in the "conflict" procedure after 12 sessions with each eye (Day 48). On Day 48, no reinforcements were programmed during the first three presentations of the VI stimulus (+) for the right eye. Details as in Fig. 2.

nation for long periods of time after the reversal of the discrimination (*e.g.*, Day 22, Fig. 3, and Day 37, right-eye session, Fig. 4) and responded appropriately in the absence of reinforcement at the beginning of a session (*e.g.*, Day 48, right-eye session, Fig. 4) suggests that the maintenance of reinforcement schedules throughout all sessions did not interfere with transfer tests.

DISCUSSION

Implicit in the design of the present experiments is the notion that what transfers is not stimuli alone or responses alone, but rather the acquired control of responses by stimuli. An adequate test of the transfer of stimulus control, therefore, should guarantee that the organism can emit the discriminative responses and will attend to the locus of the discriminative stimuli with either eye covered. One way to satisfy these criteria is to establish different discriminative performances for each eye, as in the reversal transfer procedure. Such a procedure may seem to complicate matters, but in fact it simplifies them by ruling out certain interpretations of the results (for example, to consider an extreme, it is never necessary to test whether the organism has gone blind in one eye), and provides an additional advantage in permitting repeated tests with a single organism.

In the present experiments, interocular transfer of discriminations occurred in the pigeon under all conditions of viewing. Some responding often did occur during the initial presentations of the EXT stimulus (—) in transfer tests (*e.g.*, Fig. 1). But the amount of this responding was such that it can be attributed to the greater tendency to emit responses to the EXT stimulus (—) early than late in sessions on a given day (spontaneous recovery) and, in simple transfer tests, to the novelty of the first presentation of this stimulus to a given eye as easily as it can be attributed to a partial lack of transfer.

In contrast to the present experiments, Levine's experiments (Levine, 1945a, 1945b, 1952) demonstrated interocular transfer only under certain conditions. Most of Levine's experiments used a Lashley jumping stand modified for pigeons. Each pigeon was trained with one eye covered to jump from a rotating perch to one of two platforms. Levine's distinction

between anterostral and subrostral stimuli was based on the placement of discriminative stimuli on these platforms, rather than on limitations on the visual field of the pigeon. Subrostral stimuli were located on the floors of the platforms, near the bird and below its head. Anterostral stimuli were located on the back walls of the platforms, several inches in front of the bird and slightly below its line of sight. Discriminations of subrostral stimuli transferred from one eye to the other, but discriminations of anterostral stimuli did not.

Levine also tested the interocular transfer of a discrimination of anterostral stimuli with pecking rather than jumping as the response. Two pigeons were trained with one eye covered to peck for food through a vertical yellow card but not through a vertical blue card. This performance also did not transfer to the covered eye (Levine, 1945b).

The present tests with anterior stimuli seem most analogous to this pecking test of Levine's. The present anterior stimuli, therefore, were probably equivalent to Levine's anterostral stimuli. Levine indicated, on the other hand, that anterostral stimuli, unlike subrostral stimuli, did not involve binocular viewing. Thus, the present tests with lateral stimuli may be more appropriate to compare with Levine's results with anterostral stimuli, because the goggles that limited viewing to lateral stimuli eliminated the pigeon's binocular field. In either case, interocular transfer occurred with both anterior and lateral stimuli in the present experiments. It appears, then, that an account of the difference between Levine's and the present results may depend on differences in the details of the testing procedures, rather than on differences in the parts of the visual field that were tested.

It has been argued that the pigeon is laterally far-sighted and anteriorly near-sighted, and that this characteristic of the pigeon's visual system determined Levine's results (Catania, 1964). If pigeons are laterally far-sighted, the pigeon on the jumping stand in Levine's experiments had to cock its head to the side to look at the distant anterostral stimuli, but not to look at the nearby subrostral stimuli. With anterostral stimuli, therefore, the jumping responses had to be different with either eye covered, because the pigeon had to cock its head to the right or to the left depending on which eye was covered. This necessary

change in posture when the eye-cover was switched from one eye to the other for the first time could have affected the results of anterostral transfer tests. Thus, Levine's failure to obtain transfer of anterostral discriminations may have depended in part on his use of a jumping response. Such an interpretation is not without precedent. Other studies (e.g., McCleary, 1960; Meyers and McCleary, 1964) have shown that the choice of response can be an important determinant of the results of an interocular transfer test. In the present experiments, the choice of response was less critical, because the procedures guaranteed an extensive history of pecking with either eye covered.

The present interpretation, however, does not necessarily account for Levine's failure to obtain transfer of an anterostral discrimination in his pecking test and in other control experiments. One other relevant variable may be the amount of training on a given discrimination, which has been demonstrated to affect the amount of interocular transfer (Muntz, 1961). Levine's tests involved, at most, hundreds of responses from each pigeon; the present tests involved tens of thousands of responses. Compared to Levine's pigeons, therefore, the pigeons in the present experiments may have been considerably overtrained, a factor that would strongly favor complete interocular transfer.

These comparisons imply that the presence or absence of interocular transfer depends on a variety of factors, a number of which may be peripheral rather than central. The nature of an organism's visual system, the choice of response, and the amount of training, for example, may interact to determine the results of a particular experiment.

The testing procedure itself can be a determinant of the conclusions drawn from an experiment, as is suggested by the results of the conflict procedure. In the absence of supplementary information, the successful conflict performance might have been interpreted as evidence for absence of interocular transfer in the pigeon. The pigeon's ability to respond to one discrimination with one eye and to the reversal of this discrimination with the other eye suggests that there is no interference be-

tween the input to one eye and the input to the other eye. Direct tests of transfer, however, in the present simple and reversal transfer procedures, showed that interocular transfer does occur. Thus, the conflict procedure must be interpreted as a test of conditional discrimination, in which the two eye fields or, alternatively, the different parts of the apparatus that were visible to one and to the other eye, functioned as discriminative stimuli. Successful performance in a conflict procedure, therefore, can be used as evidence for the absence of transfer only when supplemented with other information about transfer in a given organism (e.g., as in Myers, 1959, or Trevarthen, 1962).

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