

Discrimination of speed and direction of rotation in the pigeon: A mirror-image effect

DONALD J. STEHOUWER and M. RAY DENNY
Michigan State University, East Lansing, Michigan 48824

Pecks to a 15-rpm clockwise visual stimulus were reinforced on a mult VI 30-sec EXT schedule. Pecks were extinguished in the presence of: Part A, a dark key; Part B, a 10-rpm clockwise stimulus; Part C, a 15-rpm counterclockwise stimulus. In Parts A and B, the results indicated that responding to counterclockwise rotations mirrored the pattern of responding to clockwise rotations. In Part C a different pigeon learned to discriminate between clockwise and counterclockwise rotations, but generalization tests 5 and 12 days after the original tests showed emergence of the mirror effect noted in the first two parts.

Levine (1945) has demonstrated interocular transfer of monocular discrimination training from one eye to the other in the pigeon when one eye was covered during training and the opposite covered during testing. Unlike mammals, the optic nerves of the pigeon cross completely at the optic chiasma, so that each optic tectum receives direct information from only the contralateral eye (Cowan, Adamson, & Powell, 1972). Mellow (1965, 1966) stressed this anatomical fact when she found, after training pigeons to discriminate oblique lines monocularly, that generalization tests show a peak of responding at 45 deg (S+) when the trained eye was tested and, unexpectedly, a peak at 135 deg when the untrained eye was tested (interocular transfer). In no case did peaks occur at both 45 and 135 deg with monocular presentation.

A similar effect has been obtained with binocularly trained pigeons (Thomas, Klipec, & Lyons, 1966). When trained to peck at a key illuminated by a 30-deg oblique line, pigeons in subsequent generalization tests yielded peaks in the gradient at both 30 and 150 deg (the mirror image), presumably demonstrating that interocular transfer can occur without interference when both eyes are used in training. Mello (1968) found interocular transfer with vertically moving horizontal stripes in monocularly trained pigeons but equivocal results with a pattern of horizontally moving vertical stripes.

The main purpose of the present study was to test for the mirror-image effect with a rotating visual stimulus.

METHOD

Subjects

Three one-year old female White Carneaux pigeons were used. One had previous exposure to different wavelengths and line tilts, the others were experimentally naive. All were maintained at about 80% ad lib weight on a diet of mixed grain and water throughout the experiment. Typically, Ss were run every day.

Apparatus

The experimental chamber was a modified LVE small pigeon chamber. The box, measuring 34.3 cm along the intelligence

panel, was trimmed to fit the 27.9-cm ceiling, and the left and center keys were covered by aluminum plates, leaving only the right key exposed. The key was located 22.2 cm from the floor, with the food magazine situated 10.8 cm below and centered on the panel.

A projector capable of presenting a rotating stimulus was constructed, using a 27 V dc General Electric aircraft motor (Model 5BA10AJ 37B). Direction of rotation was changed by reversing polarity of the current. Speed from 0 to 20 revolutions per min (rpm) was controlled through a 100-ohm Ohmite rheostat and a simple 2-speed transmission device. The motor noise varied with speed so that it was necessary to control or check for possible auditory discrimination. The key was transilluminated by a white light through a "pinwheel" desing consisting of alternating transparent and opaque sectors, each sector being 45 deg in arc. Thus, the stimulus on the key was a rotating Maltese cross.

Procedure

As a control for the other three parts of the experiment, pecks by the experimentally sophisticated pigeon were nondifferentially reinforced on a VI 30-sec schedule in the presence of each of nine different speeds of rotation. With the counterclockwise direction designated as "negative" and clockwise as "positive," the values used were -20, -15, -10, -5, 0, +5, +10, +15, and +20 rpm. Each session consisted of 27 1-min periods during which single stimulus values were presented. These periods were separated by 15-sec blackouts with the houselights off and the key darkened. Stimulus values were presented in a pseudorandom sequence, appearing three times within each session. The pigeon received 15 sessions of training with the number of responses to each stimulus recorded in sessions 11-15. These data provided evidence for the possible presence of any stimulus preference or dynamism effect along a stimulus dimension which had never before been used in such a context. This procedure was based on those used by Honig (1961) and Blough (1959) for similar reasons.

In each part of the main experiment, keypecking of the pigeon was reinforced on a mult VI 30-sec EXT schedule. During each session, S+ and S- each appeared for 25 1-min periods alternating according to a pseudorandom sequence. Each period was separated from adjacent periods by a 15-sec blackout during which both the houselight and keylight were off. This phase continued until S had completed at least 10 sessions and had reached the criterion of 10 responses in the presence of S+ to one response in the presence of S- for 3 consecutive sessions. During the next three sessions, for all parts of the main experiment, generalization gradients for the previously listed

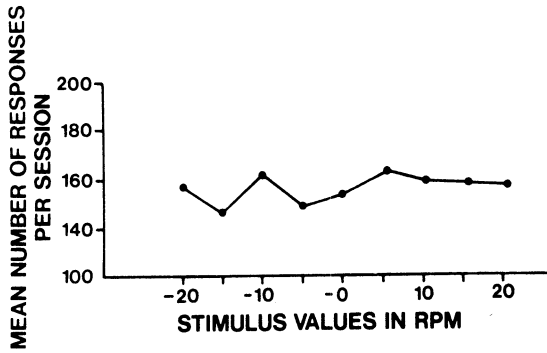


Fig. 1. Amount of responding to each stimulus value during test.

nine test stimuli were determined using a resistance to extinction technique (Guttman & Kalish, 1956). Each stimulus was presented once for a 30-sec period in each block. There were nine distinct blocks, making a total of 81 stimulus presentations per session. The order of stimulus presentation within blocks was determined by a 9 by 9 latin square so that each stimulus value appeared once in every ordinal position in a block (Jenkins & Harrison, 1960). Prior to presentation of each block, S+ was presented for 1 min, pecks being reinforced on a VI 30-sec schedule. All stimulus presentations were separated by 5-sec blackout. Reinforcement throughout consisted of a 3-sec access to grain.

Part A. Keypecking by a naive pigeon was autoshaped (Brown & Jenkins, 1968) and reinforced for each of the next 50 occurrences on the first day. The next 10 sessions consisted of discrimination training on a mult VI 30-sec EXT schedule. The S+ was a +15 rpm stimulus and S- was a dark key. The motor ran at a constant speed throughout the entire session, since the only change necessary was to turn off the stimulus light. Thus, the motor noise could not possibly have served as a cue for responding. Generalization gradients were obtained during the next three sessions.

Part B. The pigeon of Part A was trained to discriminate between +15 rpm (S+) and +10 rpm on a mult VI 30-sec EXT schedule. During this part, it was not possible to equate motor noise for S+ and S-. However, because a two-speed transmission linked the motor to the stimulus projector, the motor noise for a +10 rpm rotation was identical to that of a 20 rpm rotation, a stimulus value used in generalization testing.

Part C. Keypecking of a naive pigeon was autoshaped to a +15 rpm stimulus and reinforced for each of the next 50 responses. For the next 10 sessions, the pigeon received discrimination training on a mult VI 30-sec EXT schedule in which a +15 rpm stimulus was S+ and a -15 rpm stimulus was S-. Auditory discrimination was eliminated since the motor speed was the same for both +15 and -15 rpm. This S was also tested on a stimulus in which the number of sectors was doubled.

RESULTS

The results for the preliminary experiment are presented in Fig. 1. Responding to each stimulus over all 5 days revealed no preference for any stimulus value, nor was there any evidence for stimulus dynamism. The gradients for the individual sessions as well as the total gradient are essentially flat.

Part A.

Figure 2 presents the generalization gradients for Part A. The large curve shows the mean generalization gradient of the three individual tests (insets). From all of the gradients it is clear that there are peaks on both sides of zero at or near S+ (+15 rpm) or -S+ (-15 rpm). Also it may be noted that session-to-session responses to the counterclockwise stimuli declined in comparison to the clockwise direction. Even so, the mirror effect was maintained. From the insets of Fig. 2 it also appears that a "peak shift" developed across sessions, with the most responses occurring in the presence of a +20 rpm rotation instead of S+. A corresponding peak shift developed at -20 rpm for the counterclockwise stimuli.

Part B.

The results here are seen in Fig. 3. There is again a peak on both sides of zero at or beyond S+ or -S+. Responding to the reverse direction was generally lower than to the training direction, but the pigeon clearly learned to discriminate between -15 rpm (-S+) and -10 rpm (-S-) after having been trained only to discriminate +15 rpm (S+) from +10 rpm (S-). One can also note that the responses to stimuli between -10 and +10 rpm were consistently few in number.

Part C.

In Fig. 4 it is immediately apparent that the rate of responding was low for the S- direction and that the generalization gradient for this side is quite flat, that is, when the stimulus correlated with extinction was of equal speed but in the opposite direction to S+

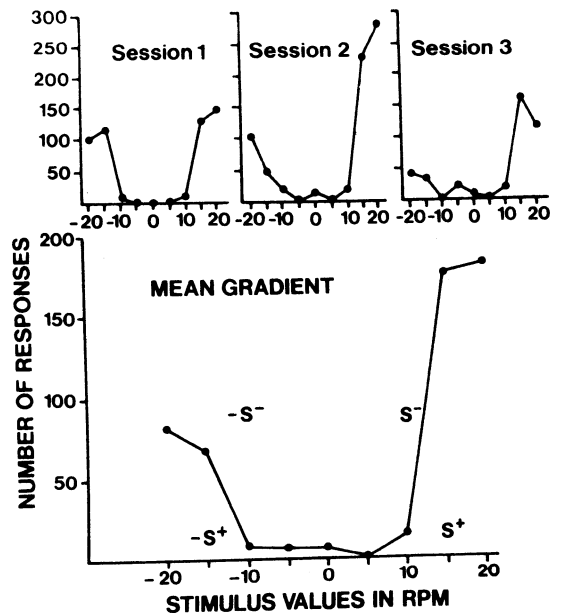


Fig. 2. Generalization gradients obtained after the pigeon has learned to discriminate between +15 rpm (S+) and a dark key (S-).

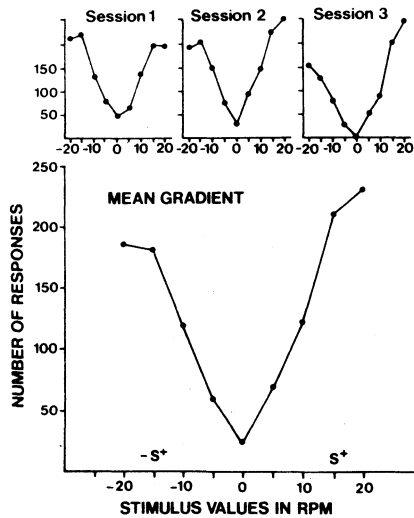


Fig. 3. Generalization gradients obtained after the pigeon has learned to discriminate between +15 rpm (S^+) and +10 rpm (S^-).

(+15 rpm). In contrast, responding for the S^+ direction shows a sharp increase away from 0 rpm, yielding a steep gradient on the positive side, together with a peak shift. Doubling the number of sectors on the stimulus display yielded, in comparison with the original display, essentially no difference in either the pattern or number of responses emitted to the different stimulus values during generalization testing (control for flicker-rate interpretation).

Five days, and again 12 days later, when retested for one session exactly as before, the pigeon yielded results as shown in Fig. 5. From reference also to Fig. 4, it can be seen that responding to the clockwise or positive stimuli did not undergo much change after 5 or 12 days whereas the gradient for the negative stimuli developed a shallow reversal of the gradient for the positive side,

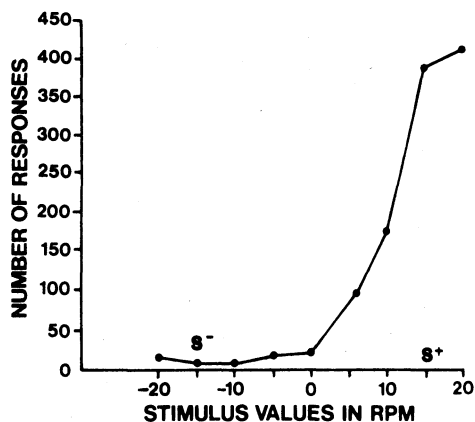


Fig. 4. Generalization gradient after the pigeon has learned to discriminate between +15 rpm (S^+) and -15 rpm (S^-).

with the most responding occurring to S^- (-15 rpm), a mirror-image effect.

DISCUSSION

Responding during the counterclockwise direction was clearly a reflection of responding during the positive, clockwise direction, especially when the SD was speed of rotation. And even when direction was the SD , the pigeon spontaneously showed the mirror effect after a 5-day retention interval. Whether this is because of ongoing interhemispheric transfer or differential forgetting of inhibition is not known.

The findings of Mello (1965, 1966) based on monocular presentation of the discriminative stimulus, indicated that mirror-image interocular transfer occurs in pigeons even though their optic nerves are completely crossed at the optic chiasma. Thus, both hemispheres presumably receive input from each eye (interhemispheric transfer). An alternative explanation is that perhaps the pigeons were attending to a particular locus on the key. In this case, rate of responding would be modulated by "flicker-rate," rather than rotation, thus yielding what appears incorrectly to be a mirror-image effect. This explanation can be discounted by considering the results of Part C. First, the pigeon responded differentially to stimuli whose "flicker-rate" was identical, e.g., +15 rpm and -15 rpm. Also, in this part, the number of sectors was doubled for one testing session, thus, doubling the relative "flicker-rate" of the stimulus. This manipulation did not alter the pattern of responding, as a "flicker-rate" interpretation would suggest.

Cumming, Siegel, and Johnson (1965), on the other hand, have proposed that, since the eyes of the pigeon are separated by only a paper-thin interorbital septum, perhaps the image is projected through the trained eye onto the back of the untrained eye (the eyes are situated back to back). This image would be dim but inverted from left to right, yielding the mirror effect. In a similar preparation, however, except that the ipsilateral rather than the contralateral hemisphere was directly activated, Noble (1968) has obtained the same mirror image in an optic chiasm sectioned monkey; that is, in an animal that does not have eyes placed back to back or a paper-thin septum, thus supporting the assertion that the mirror-image effect requires that the two hemispheres receive input from only one eye. From this it follows that the binocular presentation used in the present study presumably allowed both eyes to mediate a strong mirror-image effect.

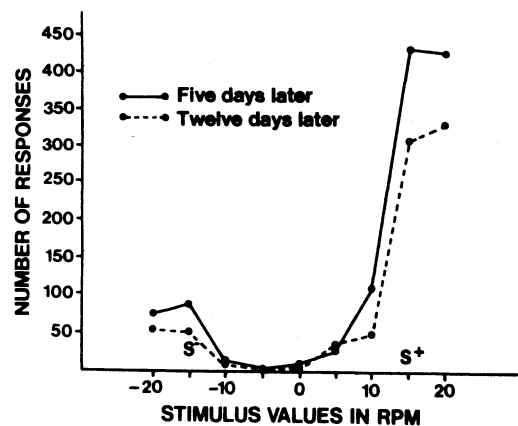


Fig. 5. Generalization gradients obtained 5 and 12 days after the gradient in Fig. 4 was obtained.

Beale and Corballis (1968) have suggested an alternative interpretation of mirror-image effects which does not involve mirror-image interocular transfer. Following monocular training, they found that pigeons directed their pecks at the side of the key corresponding to the open eye. In studies such as Mello's in which an oblique line served as S+, only the part of the line extending into the "pecked-at" half of the key would be attended to. For example, with the left eye occluded, a line at 45 deg orientation would be attended to as a line extending into the upper half of the right hemikey. Subsequent testing, with the left eye open, would yield the mirror-image effect, since now the 135-deg (mirror-image) stimulus would extend into the upper portion of the "pecked-at" (left) hemikey. Beale and Corballis's results suggest that this may be the case. Our finding with doubling the number of sectors suggests that in the present study the Ss were not attending to a specific locus on the key.

An experimental test could be made by monocularly training a discrimination with the discriminative stimuli located in the lateral field, which is presumably "panoramic," and testing for transfer to the other eye.

REFERENCES

- Beale, I. L., & Corballis, M. D. Peak-shift: An explanation for interocular mirror image reversal in pigeons. *Nature*, 1968, 220, 82-83.
- Blough, D. S. Generalization and preference on a stimulus intensity continuum. *Journal of Experimental Analysis of Behavior*, 1959, 2, 307-317.
- Brown, P. L., & Jenkins, H. M. Autoshaping the pigeon's keypeck. *Journal of the Experimental Analysis of Behavior*, 1968, 11, 1-18.
- Cowan, W. M., Adamson, L., & Powell, T. P. S. An experimental study of the avian visual system. *Journal of Anatomy*, 1961, 95, 545-562.
- Cumming, W. W., Siegel, I. M., & Johnson, D. Mirror-image reversal in pigeons. *Science* 1965, 1517-1518.
- Guttman, N., & Kalish, H. I. Discriminability and stimulus generalization. *Journal of Experimental Psychology*, 1956, 51, 79-88.
- Honig, W. K. Generalization of extinction on the spectral continuum. *Psychological Record*, 1961, 11, 269-278.
- Jenkins, H. M., & Harrison, R. H. The effect of discrimination training on auditory generalization. *Journal of Experimental Psychology*, 1960, 59, 246-253.
- Levine, J. Studies in the interrelations of CNS structures in binocular vision: II. The conditions under which interocular transfer takes place in the pigeon. *Journal of Genetic Psychology*, 1945, 67, 131-142.
- Mello, N. K. Interhemispheric reversal of mirror image oblique lines following monocular training in pigeons. *Science*, 1965, 148, 252-254.
- Mello, N. K. Interocular generalization: A study of mirror image reversal following monocular discrimination training in the pigeon. *Journal of the Experimental Analysis of Behavior*, 1966, 9, 11-16.
- Mello, N. K. Interhemispheric transfer of a discrimination of moving patterns in pigeons. *Brain Research*, 1968, 7, 390-398.
- Noble, J. Paradoxical interocular transfer of mirror image discriminations in the optic chiasm sectioned monkey. *Brain Research*, 1968, 10, 127-151.
- Thomas, D. R., Klipec, W., & Lyons, J. Investigations of a mirror-image transfer effect in pigeons. *Journal of Experimental Analysis of Behavior*, 1966, 9, 567-571.

(Received for publication July 19, 1974.)