Some Aspects of the Use of Visual Cues in Directional Training of Homing Pigeons[1]

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HYPOTHESES about how birds are able to find their way home from an unfamiliar location often require the bird to make rather precise determinations of the position and/or motion of celestial bodies—usually the Sun in the case of homing piegons. Specifically Matthews (ref. 1) suggested that a pigeon could use his hypothesized system of navigation if it could detect 0.7° difference in altitude and 1.2° difference in azimuth of the Sun. Pennycuick ref. 2) suggested 12′ of altitude and 1.5″ of arc per minute as minimum differences the bird would need to detect to use his proposed system of navigation to as little as 12 n. mi. from home. Meyer (ref. 3) reported that homing pigeons were able to discriminate a difference in altitude of a projected light of 30″, and a difference in arc angle of 1°.

This paper reports an investigation aimed at determining how accurately homing pigeons (*Columba livia*) can in fact measure the position of a light source, and what cues are used in making the measurements.

[1] This paper was presented by Klaus Schmidt-Koenig.

EXPERIMENT 1

The subjects were homing pigeons chosen from the Duke University and Wilhelmshaven stocks kept at Duke University. All pigeons except numbers 6 and 11 made successful homing flights of up to 200 km, either before or after these experiments. The birds had not previously been used in any other training work.

The technique used is similar to a method used to obtain psychophysical thresholds from a variety of animals (refs. 4 to 6). Details of the technique have been described elsewhere (ref. 7).[2] Briefly, the pigeon sat on a circular table in a small box with its head through a slit in the front of the box (fig. 1). On top of the table in front of the pigeon were two pecking keys (A and B) and a food reward cup. The pigeon was conditioned to peck key A if the position of the light source (relative to the bird's own orientation) was in a se-

[2] McDONALD, D. L.: Some Aspects of the Use of Visual Cues in Directional Training of Homing Pigeons. Unpublished Ph.D. dissertation, Duke University, 1970.

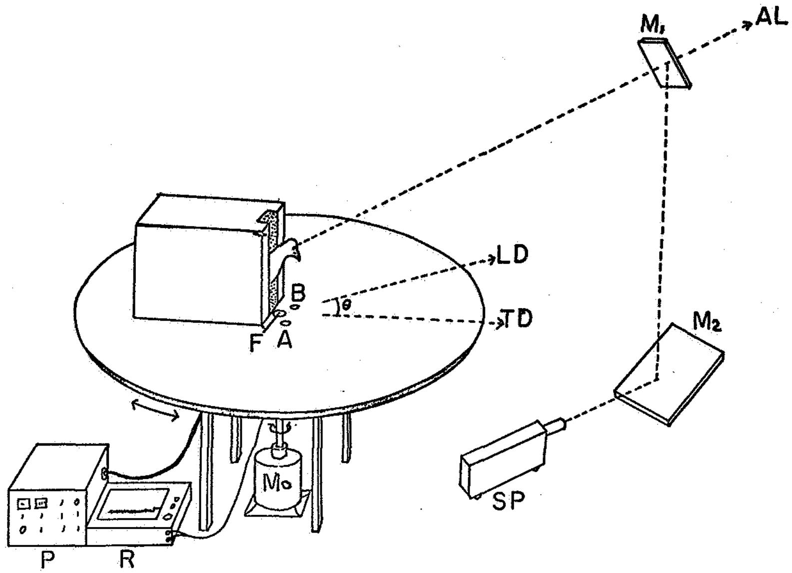

FIGURE 1. Diagrammatic representation of experimental arrangement: A and B, response keys; F, food-reward cup; LD, direction of the light; TD, trained direction; θ, angle between trained and light directions; SP, slide projector; M_1 and M_2, mirrors; AL, apparent light; P, programmer; R, position recorder; Mo, motor.

lected position called the trained position, and to peck key B if the light was not in the trained position. Pecks on key A moved the light source away from the trained position; pecks on key B, toward the trained position. Thus if the bird detected that the relative position of the light source was not in the trained position, it pecked key B, moving the light source closer to the trained position by small steps, one step for each peck. Eventually the bird was not able to discriminate the position of the light source from the trained position, and began to peck key A, moving the light source away from the trained position by small steps. This continued back and forth, oscillating about the average position which the bird could not discriminate from the trained position. The behavior was reinforced by food rewards. Four to 10 pecks were required on each key for the bird to get a food reward.

Training was quite slow. The birds were worked for about ½ hr each day. About 2 weeks of training was required until the birds showed signs of learning the discrimination. The entire experiment took 35 to 45 days from start of training until the data had been collected.

The light source used was a slide projector utilizing a 500-W lamp. The slide projector sat on top of a large truncated cone made from a metal frame covered by white cloth (fig. 2). The light was projected onto the bird through a series of seven mirrors. By moving its head through a maximum of 7.5 cm to each side, the pigeon observed a paralax movement of only 1°.

During nearly every training session, a diagnostic test was performed to check on whether the pigeon was in fact using the relative position of the light source as the cue for the discrimination. The test was per-

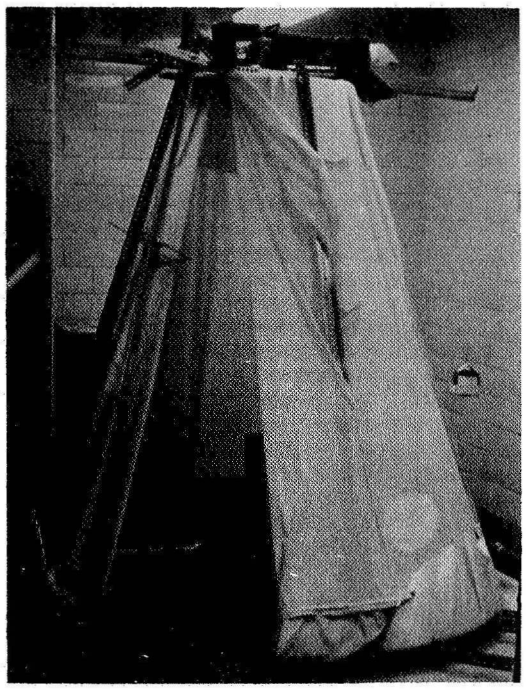

FIGURE 2. Slide projector used as light source is mounted on top of framework. Rotating table and pigeon's box can be seen through folded-back sheet which zipped closed when the birds were working. Small arrow points to last mirror in the series, which could be moved up and down the track on which it is mounted to change the altitude of the light.

formed by moving the light source far away from the position at which the pigeon had set it. The bird was correctly performing the discrimination if it immediately reset the light source to its pretest relative position (fig. 3).

A continuous record of the orientation of the table was made by plotting on a recording (VOM) the resistance of a precision potentiometer coupled to the rotation of the table. The orientation of the table could be read to 0.1° of the true orientation.

In order to calculate an average direction about which the pigeon oscillated, a frequency distribution of the number of times the table was pointed in different directions was constructed. This was done by counting the number of times the recorded trace crossed each of the lengthwise lines on the chart paper. These lines were approximately 0.286° apart, giving 0.286° per class interval.

Results

The pigeons were trained to adjust the relative position of the light source to three different positions.

(1) The trained position of the light source for pigeons 6 and 11 was 62° relative azimuth counterclockwise from the longitudinal axis of the box in which the pigeon sat. The relative azimuth of the light source was changed by rotating the table on which the bird was placed. Pecks on key A rotated the table counterclockwise; on key B, clockwise. (The altitude of the light source was held at a constant 21°.) Pigeon 6 could discriminate the relative azimuth of the light source from the trained position when they differed by only 3.4°, on the average. Pigeon 11's performance was similar, discriminating a difference of 3.6°.

(2) The trained position of the light for pigeons 121 and 122 was 19° altitude above horizontal. Pecks on key A moved the altitude higher than 19°; on key B, closer to 19°. (The light remained a constant 40° clockwise for these birds.) Pigeon 121 could discriminate the altitude of the light from the trained altitude when they differed by as little as 8°; Pigeon 122, when they differed by as little as 11°.

(3) The trained position for pigeon 51 was 40° relative azimuth clockwise and an altitude of 21°. Pecks on key A rotated the light clockwise around the bird (by rotating the entire cone) and raised the altitude; pecks on B rotated the light counterclockwise and lowered the altitude. The movements

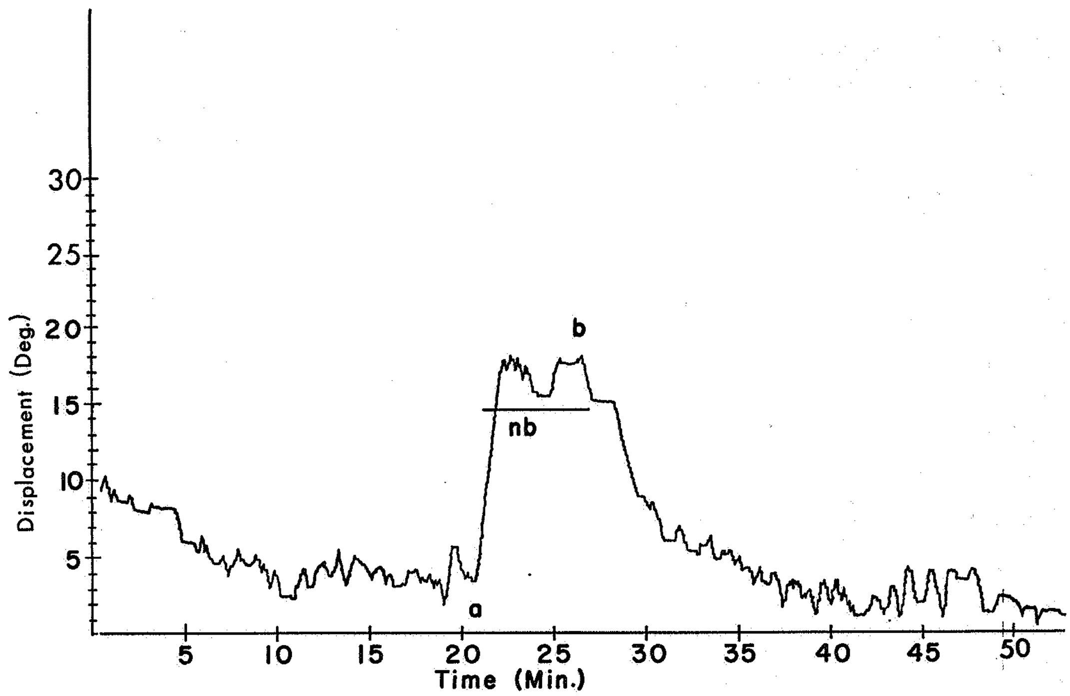

FIGURE 3. Example of correct response in a diagnostic test. At point a, light source was rotated 14.5° counerclockwise around the pigeon; nb, the new baseline. Bird quickly resets relative position between itself and light source to what it was before light was moved. At b, light was returned to original position, and bird again adjusts correctly.

were directly coupled. Pigeon 51 adjusted the light on the average to 5.1° difference from the trained relative azimuth and 9.0° from the trained altitude. Investigation showed that only the altitude of the light source was being used for the discrimination. If the relative azimuth were held constant, the bird would adjust the altitude in a normal manner; but if the altitude was held constant and the relative azimuth alone allowed to vary, the bird became confused.

The results are tabulated in table 1.

Discussion

The data collected here do not compare favorably with the limits of 0.7° difference in altitude and 1.2° difference in azimuth that Matthews (ref. 1) suggested a pigeon would need to detect. Neither do they compare well with the 12′ difference in altitude suggested by Pennycuick (ref. 2). The results are also not as good as those reported by Meyer (ref. 3), where pigeons could discriminate a difference of 30′ altitude and 1° azimuth. As will be shown next, the use of shadows was important in the discriminations reported here. It is doubtful if shadows were important in Meyer's study, since the light was projected onto a screen rather than onto the bird itself. Thus the birds could well have been responding to different stimuli in the two studies.

Observations on Pigeon 6

Careful observations were made of pigeon 6 while it was working in the apparatus. The observations were made through a small peephole without disturbing the pigeon. This pigeon always drew its head inside the box and pecked on the inside wall between pecks on the response keys. These movements resembled superstitious behavior; i.e., irrelevant behavior patterns that are maintained by inadvertent reinforcement. However, closer observations suggested that the pigeon was directing the pecks at a small lighted area on the inside wall of the box, which was illuminated by light passing through the slot in the front of the box (fig. 4). This lighted area moved along the wall in correlation with the rotation of the table, and thus was a potential source of cues that could be used for the discrimination. To test this idea, a panelescent light was installed on the inside wall of the box. This light is a thin panel that emits a soft green light when connected to a power source. When the panelescent light was turned on, the contrast between the above described lighted area and the rest of the wall was obliterated. The pigeon was kept in the box with the light on for several hours so it would become accustomed to its presence. Also the bird was worked for five sessions with the panel in place but its light off to make certain that the presence of the panel did not affect its performance. Figure 5 shows the results of one test when the panelescent light was turned on during the normal working session of the bird. Three such tests were done, each with the same results; i.e., the pigeon pecked key A continuously

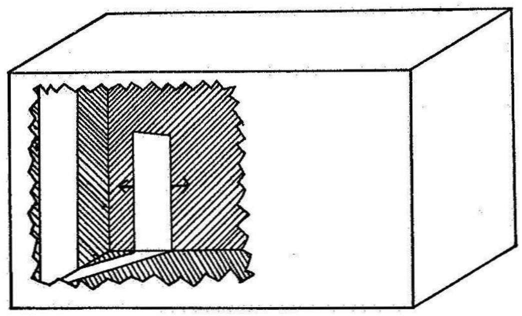

FIGURE 4. Cutaway drawing of the training box, showing lighted area to which pigeon 6 was attending. As the box rotated, lighted area moved along inside wall of the box in direction of arrows; width of lighted area varied with rotation.

TABLE 1.—*Average Performances of Pigeons in Experiment 1*

Pigeon number	n[a]	Azimuth (degrees)		Altitude (degrees)	
		x		x[b]	Sx[c]
6	7	3.4	0.5	....	
11	31	3.6	1.5	....	
51	14	5.1	1.8	9.0	....
121	10	....		8.0	2.9
122	7	....		11.0	2.8

[a] Number of trials, where each trial is the average performance during a day's session of ½ to 1 hr

[b] Average difference between the actual position and the trained position of the light source that the pigeon could discriminate. The average performance for a single day was used as one datum in calculating x

[c] Standard deviation of the n trials

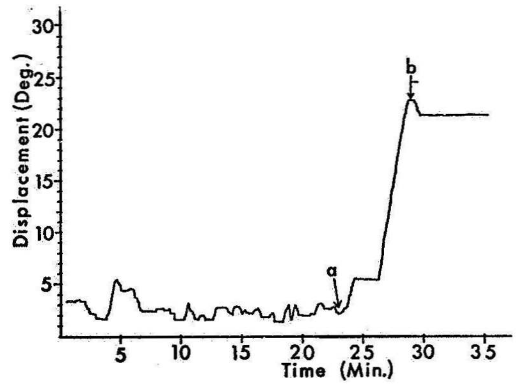

FIGURE 5. Result of turning the panelescent on for pigeon 6. At point a light was turned on; at point b, off.

after the panelescent light was turned on. The behavior of pulling the head inside the box and pecking on the wall also disappeared.

Three other tests were done in which a panelescent light on the opposite wall from the lighted area was turned on. This had the effect of dimming the contrast between the lighted and unlighted areas, but not obliterating them completely. The response was similar to the previous tests in that the bird pecked only key A. However, the pecking behavior on the inside wall continued, although the pecks were directed at the inside front corner of the box.

This evidence indicated that the stimulus to which the pigeon was attending was the position of the lighted area on the wall of the box. Thus the pigeon would observe that when it pecked key A, the area would move toward the back of the box; key B, toward the front. When the panelescent lights were turned on, it appeared as if the area had moved to the extreme forward edge of the wall, even beyond the trained position. This would lead to the continuous pecks on key A.

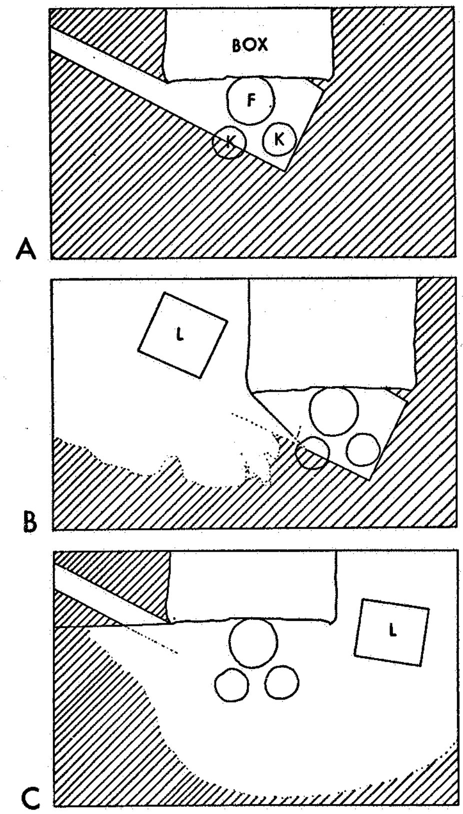

FIGURE 6. Shadow patterns for pigeon 11 (looking down on top of box and table). (A) Normal pattern at training direction. (B) Pattern with light on right side of box. (C) Pattern with light on left side of box. K, pecking key; F, food cup; L, 6-W electric lamp.

Observations on Pigeon 11

Pigeon 11 rarely pulled its head inside the box as did pigeon 6. However, the bird frequently appeared to look at the outside right front corner of the box. This led me to suspect that the pattern of the shadows on the top of the table might be supplying cues to the bird. The normal configuration of the lighted area had a long bar of light that projected past the box. This bar of light varied in width and angle to the box as the table rotated, and seemed a likely candidate for a source of cues (fig. 6A). A 6-W electric lamp was mounted on the outside of the box in such a way to obscure this lighted area (fig. 6B). When this lamp was turned on, the bird responded by pecking on key A, which seemed to confirm the importance of this cue. However, when the light was mounted on the left side of the box so as to obscure all of the lighted area except the bar projecting past the box (fig. 6C), the pigeon still pecked key A continuously.

Taking a different approach, the configuration of the lighted area was changed as in figure 7B. This increased the width of the bar of light from 15 mm to 35 mm. The bird responded by pecking key A until it was

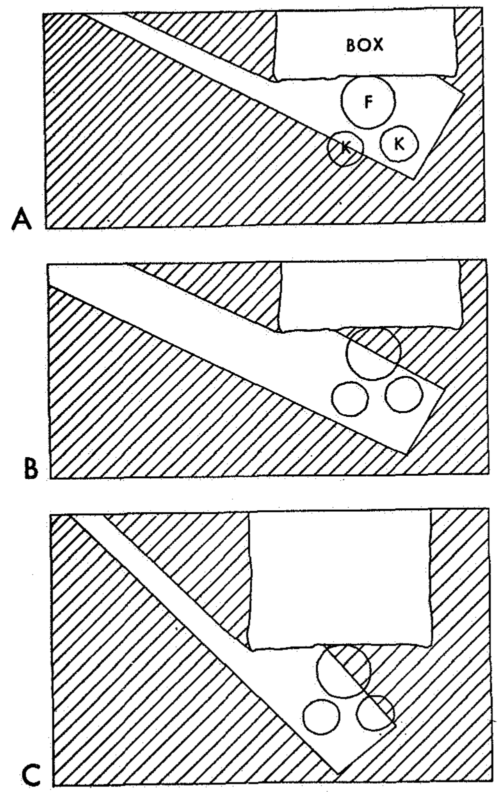

FIGURE 7. Effect of changing shape of lighted area for pigeon 11. (A) Normal shape of lighted area at training direction. (B) Experimental shape of lighted area at training direction. (C) Shape of lighted area after stabilization under experimental conditions.

about 19° from the training direction. At his position, the pattern of shadows was as shown in figure 7C. The width of the bar of light was about 16 mm, close to the width at the trained direction under normal condition. However, the angle between the box and the bar of light was 19° less than normal.

Inspection of figure 6 reveals that there is a small part of the lighted area directly in front of the right front corner of the box that was obscured when the 6-W light was on both the right and left side. This is the same location at which the bird seemed to look between pecks. The width of the lighted area at this location may well be the cue to which the bird was responding. If the area was too narrow, the bird pecked key B, rotating the table clockwise and making the bar wider. If the bird could not discriminate the width of the area from the width when at the trained direction, it would peck key A. In figures 7B and C, the lighted area was much wider than normal, seemingly indicating that the table was well beyond the trained direction. This would lead to continuous pecks on key A, which was observed.

Observations on Pigeon 121

Pigeon 121 pecked at the cover over key A between responses. It was noted that a shadow was cast on this cover by the edge of the hole in the table through which the key was pecked. As the altitude of the light changed, the edge of the shadow moved across the cover. When the altitude was 10° above the trained altitude of 19°, the edge of the shadow was 4 mm from the edge of the hole opposite the light.

A piece of black paper 9 mm high was placed on the edge of the hole nearest the light so that the entire cover over key A was in shadow. The pigeon responded by positioning the light to 50° altitude (fig. 8). The edge of the shadow, now cast by the top edge of the black paper, was found to be slightly greater than 4 mm from the edge of the hole. Thus the pigeon seemed to be attending to the position of the shadow on the cover over key A, and not directly to the altitude of the light source.

EXPERIMENT 2

Evidence was presented above that pigeons 6, 11, and 121 attended to the shadow patterns in making their discriminations. This

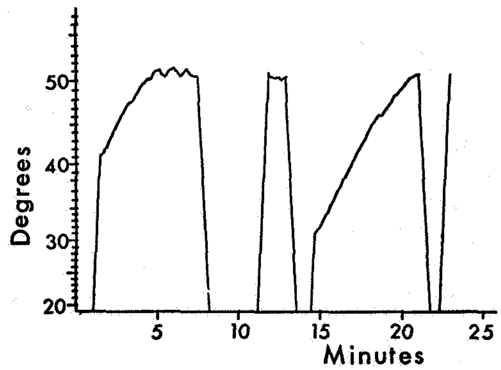

FIGURE 8. Response of pigeon 121 to changes in shadow pattern. Under normal conditions, pigeon oscillated about 27°. Each time recording line fell to 19°, pigeon was given a food reward to maintain responding.

TABLE 2.—*Response of Pigeons When All Shadows Were Eliminated and the Relative Position of the Light Source Was Changed*

Test	Response when lights on				Response when lights turned off			
	Pigeon number				Pigeon number			
	11	51	121	122	11	51	121	122
1	C	C	B	B	A [a]	A	A [a]	A [a]
2	C [b]	B	C	C	A [a]	A	A	A
3	B	B	D	C	A	A	A	B
4	C	C	B	C	A	A	A	A [a]
5	B	C	D	C	A	A	A	A

Notes:

A—Returned light to normal position. In the case of pigeon 11, the table was rotated rather than the light being moved.

B—Did not return light to normal position but continued to peck keys, keeping the light in about the same position

C—Pecked continuously on key A or B, driving the light far beyond normal position

D—Did nothing

[a] The pigeon had started to return the light but was interrupted by termination of the experiment

[b] Results of this test were ambiguous.

experiment was performed to verify that shadows were indeed important for these birds (except pigeon 6, which was not available for the experiment), and to investigate whether shadows were also being used by pigeons 51 and 122.

Apparatus

The apparatus was set up as in Experiment 1. In addition, two 15-W flourescent lights were placed under the table. When these lights were turned on, the inside of the cone was indirectly lighted, and the shadows on the table top were obscured so that they were invisible to the human eye.

Procedure

The experiment lasted 10 days. On the first day, and alternate days thereafter, the birds were worked as usual, with diagnostic tests being done to verify they were under control of the light stimulus. On the second day, and alternate days thereafter, the indirect lighting was turned on at the same time as the relative position of the light source was changed for the diagnostic test. After the nature of the bird's response became clear, the indirect lighting was turned off again, and the bird's response noted.

Results

The results are presented in table 2. In every case, the pigeons did something other than return the light to its normal relative position when the indirect lighting was on. Usually the pigeons continued pecking after the flourescent lights were turned on, indicating that they were not unduly startled by turning the lights on. Two exceptions are tests 3 and 5 for pigeon 121, where the response of doing nothing could be interpeted

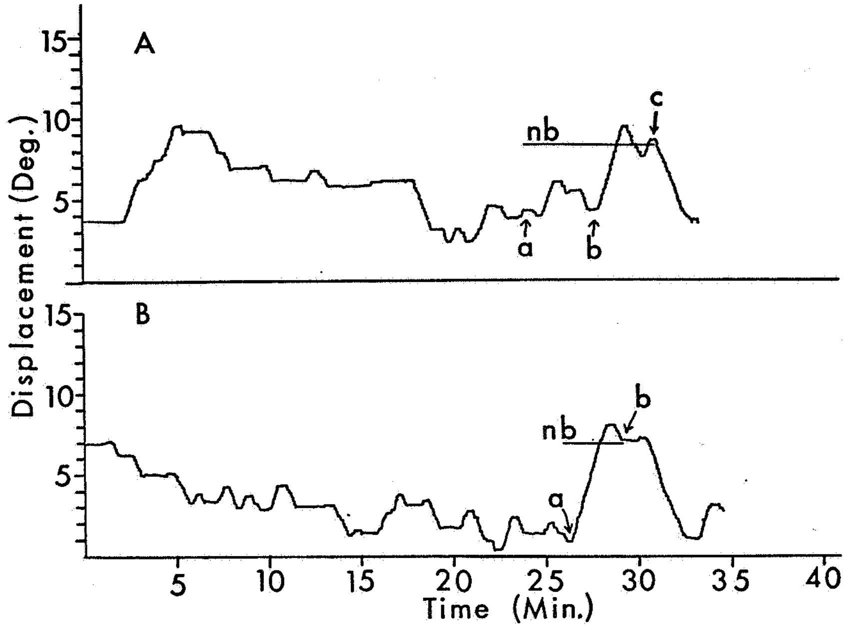

FIGURE 9. Typical response of pigeon 11 in experiment 2. A: At point a, indirect lighting was turned on, and the stimulus light moved 8° counterclockwise to new baseline (nb). At point b, indirect lighting was turned off, and the pigeon reset the table to near normal position. At point c, stimulus light was returned to original position, and pigeon appropriately reset the table. B: At point a, stimulus light was moved 7° counterclockwise, but indirect lighting was not turned on. The bird immediately responds to reset the table. At point b, table was returned to original position.

as a startle response. Distress calls were also noted in these two cases.

The reaction of the pigeons when the indirect lighting was turned off was dramatic. In all but one case, they returned the light to the normal position. Often this response began immediately after the indirect lighting was turned off, and the bird pecked the correct key rapidly and without interruption until the light was in the normal position (fig. 9).

EXPERIMENT 3

The purpose of this experiment was to see how well pigeons could measure the angle between their position and the direction of a light source in a shadowless environment. The task was identical to that for pigeons 6 and 11 in Experiment 1 so comparisons could be made.

Subjects

Three homing pigeons from the Duke University stock of pigeons, numbers 89, 94, and 95, were used. All birds were experimentally naive and had never made a homing flight.

Apparatus

The apparatus was that used in Experiment 1, except the indirect lighting used in

Experiment 2 was on at all times. In addition, two layers of cheesecloth surrounded the table upon which the bird sat in order to obscure details on the inside of the surrounding cloth that might be used as cues by the bird. The light from the slide projector could be readily seen through the cheesecloth.

Procedure and Results

The training procedure was like that used in Experiment 1. The three pigeons quickly learned to peck keys A and B for food rewards, but when changing of the pecking behavior for A and B was attempted, learning became very slow. After a total of 9½ hr of training, the birds had each learned to peck key B twice and be rotated to the training direction, then peck key A twice for a food reward. However, when the number of pecks required on each key was increased, the pigeons became confused and their responses rapidly extinguished. This suggested that they had merely learned that two pecks on key B followed by two on key A would yield a food reward. Also, when the stimulus light was rotated around the birds in a diagnostic test, the pigeons did not reposition the table to maintain the trained relative azimuth. Even when the stimulus light was turned off, the pigeons continued to peck in the same manner as when it was on. How much more training would have been required to learn the task is not known. It is possible that the addition of the cheesecloth between the bird and the stimulus light is responsible for the slower learning.

For purposes of comparison, an average of 7 hr of training was required for pigeons 11, 51, 121, and 122 to successfully learn to peck twice on each key to get a food reward. More important, diagnostic tests indicated that these birds were correctly responding to the relative azimuth of the stimulus light (or as shown in Experiment 2, the shadow patterns).

CONCLUSION

The experiments above provide conclusive evidence that all of the birds trained indoors were attending to shadows and suggests that the use of shadows may be a basic mechanism by which homing pigeons derive cues from a light source such as the Sun. This is supported by the evidence in Experiment 3, which suggests that learning to orient in a shadowless environment may, at the least, be more difficult than when shadows are present. In addition, these experiments raise the question of whether the many other experiments done in orientation cages also involved the use of shadows as cues. Training work done by Kramer (ref. 8) with starlings, Kramer and Riese (ref. 9) with pigeons, von St. Paul (ref. 10) with Western Meadowlarks, and Hoffmann (ref. 11) with starlings all involved the use of the same type of orientation cage. This cage had 12 feeders arranged around the periphery of the apparatus and a wire frame to hold up the netting. In all of these cases, whether used indoors or under natural skies, distinct shadows that could have been used by the birds for orientational cues were undoubtedly available. Even the bird's own shadow could give the same kind of directional cues. The apparatus that Matthews (ref. 12) used for indoor directional training (relative azimuth to a 60-W light bulb) would have had many shadows. Hamilton (ref. 13) reports that directionally trained ducklings were disoriented when they could not see the Sun directly but still could see the shadows on the walls of the apparatus. Also it appeared that the ducklings intentionally walked into the sunlight before making a directional choice.[3]

[3] Personal communication with W. J. Hamilton.

However, the shadow patterns on the floor or those cast by the duckling itself would also disappear when the Sun was too low, and the possibility cannot be excluded that these were used for orientation. The directional training experiments done by Schmidt-Koenig (refs. 14 to 16) using a different technique also allowed the possibility of shadows giving directional cues.

On the basis of the evidence presented here, it is impossible to say whether the use of shadows for the directional discriminations has any relevance to the mechanisms used by pigeons in homing flights. It might well be argued that when birds are directionally trained, they simply perform the task that has been taught to them. If shadows are available, the birds may learn to respond to them even if shadows play no role in homing orientation or navigation.

Most of the evidence in orientation work that implicates the position or motion of the Sun as important for orientation would apply equally well to shadows. Seldom is the Sun visible without casting shadows. The compensation for the daily movement of the Sun could well be compensation for the movement of shadows. The kinds of orientation schemes proposed by Matthews (ref. 1) or Pennycuick (ref. 2) could apply equally well to the use of shadows. The hypotheses would then suggest that the pigeons learn the length and orientation of shadows at the release site, and fly in a direction that would return the observed shadows to the same conditions as remembered for home. The shadows could be those cast by trees or buildings or even the shadow cast by the bird itself. (The bird would need to adjust for the height of objects casting the shadows.) If the bird were measuring the changes in the altitude of the Sun, using the length of the shadows would exaggerate the movement. For example, let us assume the bird wishes to measure the movement of the Sun at 8:00 a.m. at equinox at 36° N latitude. At 8:00 a.m. the altitude is 23° 52'. Four minutes later the altitude is 24° 38'. Thus the altitude of the Sun changes through a visual angle of 46'. Now let us further assume that the bird is flying at treetop level 20 m above the ground. At 8:00 a.m., a tree 20 m tall casts a shadow 45.2 m long; and at 8:04 a.m., the same tree casts a shadow 43.6 m long. The length of the shadow decreases by 1.6 m, which subtends a visual angle of 4° 34' for the bird flying at 20 m. Thus the visual angle subtended by the movement is nearly six times larger when shadows are used instead of viewing the Sun directly.

If the use of shadows is merely an artifact of experimental conditions, it is a variable that will require rigorous control in future directional training work.

ACKNOWLEDGMENT

This work was supported by an NIH Predoctoral Fellowship (1–F1–GM–37, 712), an NIH Physiology Traineeship (5T01 HE05219) under the direction of Knut Schmidt-Nielsen, two NIH research grants (MH04453, HD02319) to Peter H. Klopfer, an ONR contract (NONR 1181) to Peter H. Klopfer, and a NASA contract (NGR 34–001–019) to Peter H. Klopfer and Klaus Schmidt-Koenig.

DISCUSSION

NORRIS: Are there any studies that would reflect which way a pigeon looks when flying? Is it possible that they would be disoriented when prevented from looking down, for instance?

SCHMIDT-KOENIG: There are preliminary accounts of some experiments that we are in the process of doing. If you block the pigeon's view by blackening the lower half of its eye, it is still almost as good as the control.

CARR: Are there any experiments that actually have tested discrimination of the rate of change in angles by a process of remembering a former position and comparing it with a new position?

SCHMIDT-KOENIG: Meyer's work has some relation to this.

BULLOCK: It is known that some invertebrates can detect very slow movement, slower than the Sun across the sky. Several kinds of animals have been studied and shown to do this in behavioral as well as physiological experiments including cephalopods, locusts, and crabs. There are also experiments in which the animals' memory of the position of an object is sufficient to be able to detect a small change in position that took place during a period up to minutes in the dark.

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