THE EFFECT ON PIGEON HOMING OF ANESTHESIA DURING DISPLACEMENT

CHARLES WALCOTT AND KLAUS SCHMIDT-KOENIG

DESPITE an enormous proliferation of experimental attempts to explain the homing of pigeons, some basic questions have remained unanswered. For example, when does a pigeon obtain its navigational information? Sun navigation as proposed by Matthews (1968) and Pennycuick (1960) would require the bird to collect the navigational information upon release. Inertial navigation as proposed by Barlow (1963) postulates the acquisition of navigational information continuously during the displacement process. An experiment that might indicate whether or not pigeons obtain navigational information en route to the release site is to displace birds while fully anesthetized. Although similar experiments have been carried out with negative results (Exner, 1893; Kluijver, 1935; Griffin, 1943; and probably a few more not reported in the literature), we both independently considered it worthwhile to repeat such an experiment and, after we had found each other on the same track with essentially identical results, agreed to publish jointly.

MATERIALS AND METHODS

Experiments in Western Germany (Schmidt-Koenig).—Two releases were carried out under sunny conditions in the summer of 1961 with a total of 36 moderately experienced experimental and 38 similar control birds from the Wilhelmshaven colony, each bird being used only once in this experiment. The release site was Ahlhorn, 70 km south of the loft. In each case the experimental birds were fully anesthetized with Nembutal i.m. and immediately transported to a shelter near the release site where all but one recovered. Full anesthesia lasted for about 2 hours. The controls were injected with the same dose of Nembutal at the shelter. Two days later all birds were released in the usual manner (e.g. Schmidt-Koenig, 1964, 1965a). Initial orientation and homing performance were recorded as chief criteria. Initial orientation was assayed statistically for differences between experimental and control birds by the Watson test (Watson, 1961, 1962), homing performance by the Mann-Whitney-U test (e.g. Siegel, 1956).

Experiments in the United States (Walcott).—Five releases were carried out under sunny conditions in the summer of 1970. We used 60 birds of varying experience, 29 controls and 31 experimentals. As far as possible a bird serving as an experimental on one release was used as a control on the next release; thus the experiments compared the homing performance of the same group of birds. Each release was made from a different site in different directions from the loft; no bird had ever been released before at any of these sites.

Experimental birds were injected with Equithesin (Jensen-Salsbery Laboratories, Kansas City, Missouri) at a dose level of 0.20 cc/100 g body weight. This dose produced complete anesthesia for about 2 hours as judged by the absence of movement of the nictitating membrane when the eye was opened. Control birds were

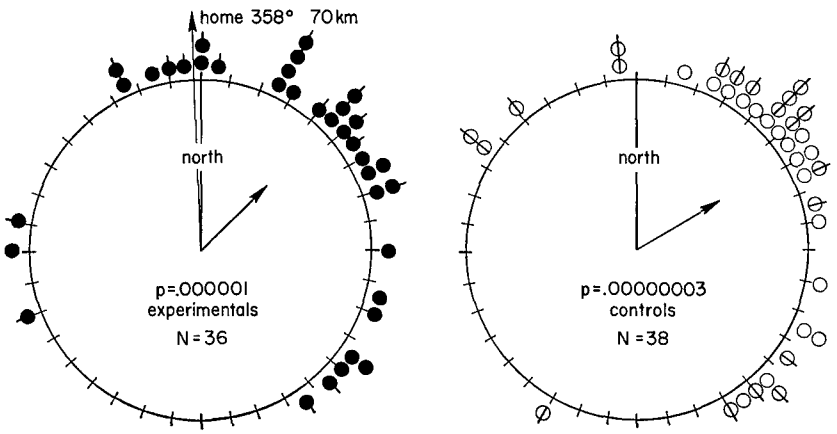

Figure 1. Summary of initial orientation (circular diagrams) of experimental birds (solid symbols) and of control birds (open symbols) released on two occasions 70 km south of Wilhelmshaven. Each symbol represents the record of one bird, the circles with lines through them represent a release on 1 August 1961, the plain circles a release on 19 July 1961.

simply taken from the loft and not anesthetized. Experimental birds were transported to the release point in closed containers, in the back of an automobile, inside a large Helmholtz coil that produced a uniform but fluctuating magnetic field of 0.8 gauss. Control birds were carried in the same car, but outside the Helmholtz coil. Both experimental and control birds were held overnight at the release point and the following day were released and tracked by radiotelemetry. The bearings given in the diagrams are the direction in which the radio signal disappeared; a distance of about 10 miles from the release point. Data were analyzed in the same way as Schmidt-Koenig's.

RESULTS AND DISCUSSION

The results of all releases are presented in Figures 1 through 4. An analysis of the results shows that neither the accuracy of the initial orientation nor the overall homing speed was significantly affected by any aspect of the experimental treatment.

Our results confirm previous reports (cited above) that displacement under heavy or full anesthesia has no appreciable effect on homing. Unfortunately the conclusion to be drawn from this evidence is not equally clear-cut. The basic idea underlying the experiment was that the pigeons may derive navigational information while being displaced and that this process may be affected by anesthesia. The negative result actually obtained does not resolve the issue. It could be that the birds even while anesthetized will obtain information on the way to the release

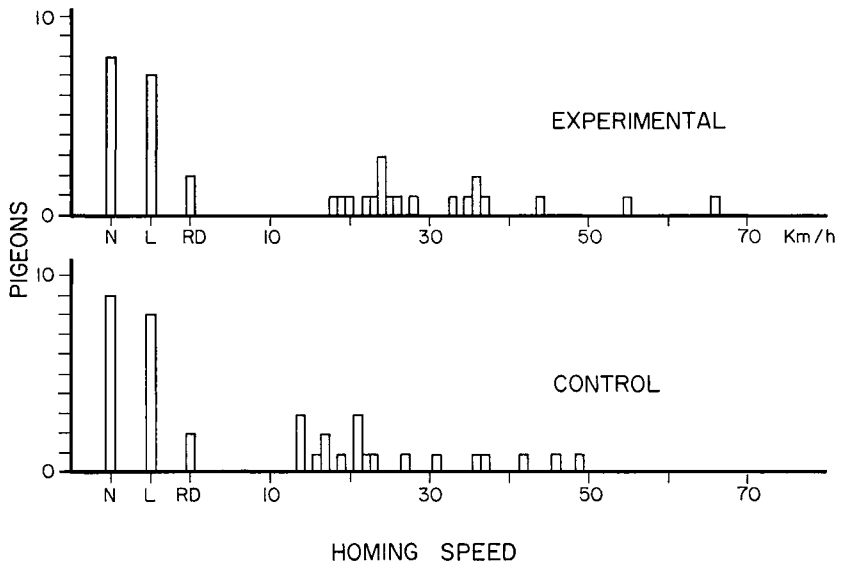

Figure 2. A comparison of the homing speeds of the experimental and control pigeons. N is the number of birds that never returned to the loft, L is the number that returned on days following the release day, and RD is the number that homed on the day of release, but slower than 10 km/hr.

point, or if the birds were deprived of this source of information they simply switched to an alternate system. Our experiments do not, therefore, exclude the possibility of inertial navigation, or of the pigeons obtaining other information on the trip to the release point, but they do make it seem less likely. Additional evidence tends to support the idea that navigational information is obtained at the release point rather than during displacement.

Schmidt-Koenig (1965a) analyzing the process of initial orientation found a measurable and steady development of headings between about 20 seconds after release and before vanishing. These observations support the view that navigational processes take place during the first few minutes or kilometers upon release. These observations have been extended in tracking experiments by Walcott and Michener (Walcott, 1971), in which they found a steady decrease in the scatter of initial orientation of pigeons between 1 and 15 miles after release.

A large number of observations (c.f. review by Schmidt-Koenig, 1965b, and as recently as Keeton, 1970) have shown that each release site has its own characteristic home error: that is, birds released at a particular site do not head exactly in the correct direction to the loft, but rather

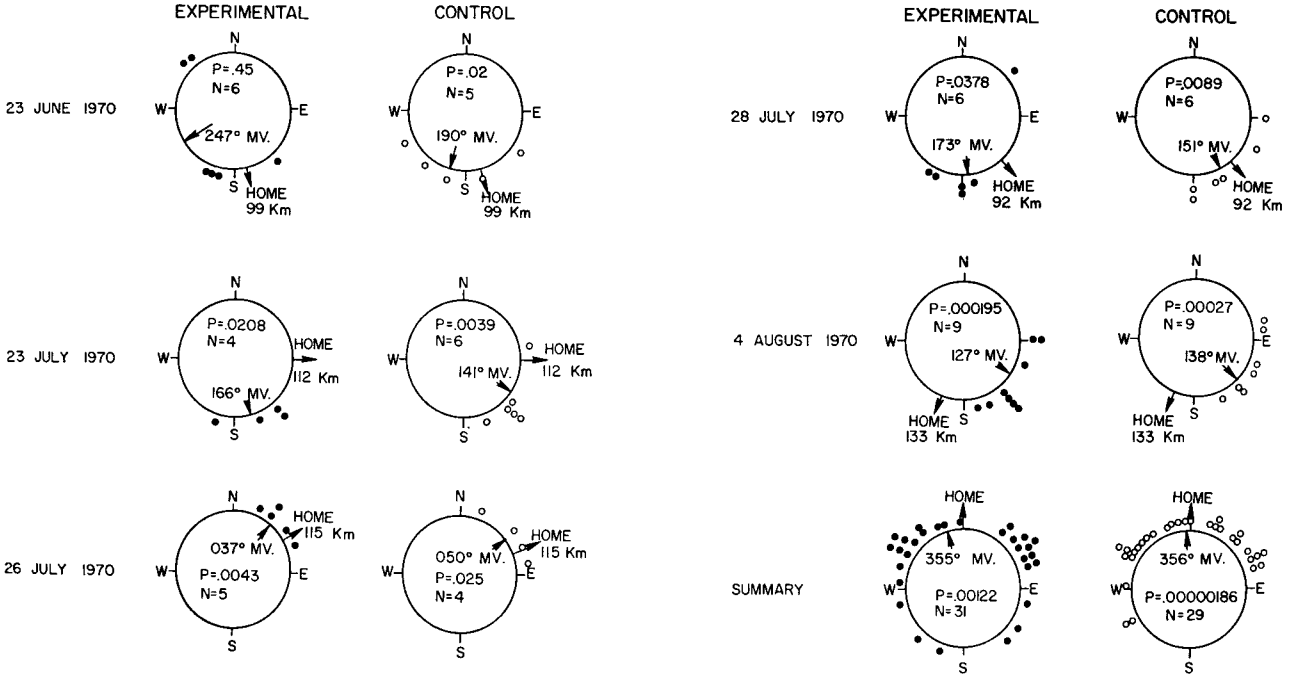

Figure 3. The results of five releases in various directions from the loft. On each circular diagram, a dot or circle represents the direction of a vanishing bearing determined by radio at about 10 miles from the release point. The "P" in the center is the probability that a given distribution arose by chance (Rayleigh test). The mean vector of each distribution is shown by an arrow inside the circle, the direction to the home loft by an arrow outside the circle. In the two distributions at the bottom summarizing the results for all the releases, all the distributions are turned so that the home directions coincide, and the vanishing points are plotted so that the home direction is at the top of the circle. Comparing all the experimental releases with all the control releases using the Watson test indicates that they are not significantly different ($P < 0.5$).

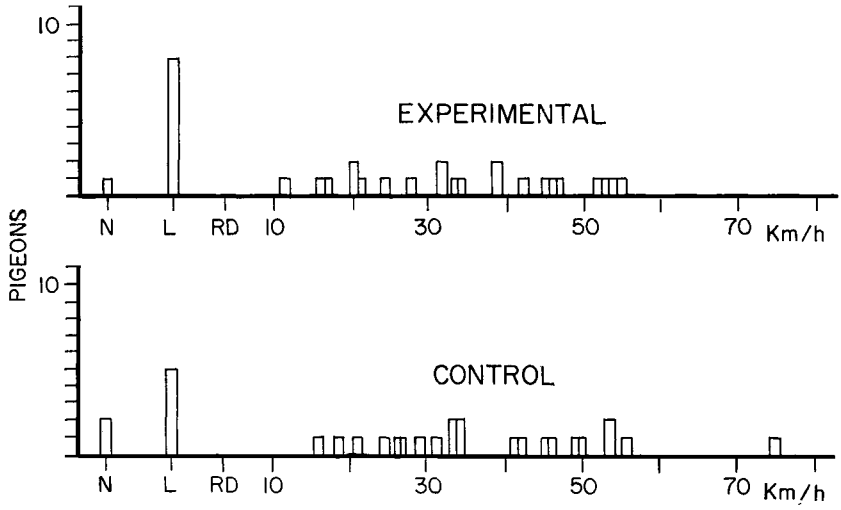

Figure 4. A comparison of the homing speeds of the experimental and control birds. There is no significant difference between the two distributions. The symbols are the same as in Figure 2.

head left or right of the true direction. This error, which ranges from only a few degrees to as much as 180°, is usually consistent from day to day and is different for pigeons returning to lofts in different directions from the release site. Thus consistent home errors at release sites also argue that pigeons obtain some sort of information at the site.

Finally, Wallraff (1965) surgically severing the horizontal semicircular canal of the pigeons' vestibular apparatus—the likely sensory organ for inertial navigation—found no effect on homing in a small series of experiments.

Furthermore, it has been commonly reported in the pigeon racing literature that pigeons that have been away from an old loft for a period of years will return to the old loft on being released. It is hard to imagine how birds could have remembered detailed directions of their displacement from the old loft over a period as long as years.

All the evidence taken together, although not fully conclusive, does tend to indicate that pigeons probably obtain navigational information upon release and during the trip home rather than during displacement.

ACKNOWLEDGMENTS

The experiments in Germany were supported by the Deutsche Forschungsgemeinschaft, and in the United States by the National Institute of Health, Division of Neurological Diseases and Stroke, Grant No. ROINSO 8708-02.

LITERATURE CITED

BARLOW, J. S. 1963. Inertial navigation as a basis for animal navigation. J. Theoret. Biol., 6: 76–117.

EXNER, S. 1893. Negative Versuchsergebnisse über das Orientierungsvermögen der Brieftauben. Sitz. Ber. Akad. Wiss. Wien, 102: 318–331.

GRIFFIN, D. R. 1943. Homing experiments with Herring Gulls and Common Terns. Bird-Banding, 14: 7–33.

KEETON, W. T. 1970. Distance effect in pigeon orientation: an evaluation. Biol. Bull., 139: 10–519.

KLUIJVER, H. W. 1935. Ergebnisse eines Versuches uber das Heimfindevermogen von Staren. Ardea, 24: 227–239.

MATTHEWS, G. V. T. 1968. Bird navigation, 2nd ed. Cambridge, England, Cambridge Univ. Press.

PENNYCUICK, C. J. 1960. The physical basis of astronavigation in birds. Theoretical considerations. J. Exp. Biol. 37: 573–593.

SCHMIDT-KOENIG, K. 1964. Uber die Orientierung der Vogal; Experimente und Probleme. Naturwissenschaften, 51: 423–431.

SCHMIDT-KOENIG, K. 1965a. Current problems in bird orientation. Pp. 217–218 in Advances in the study of behavior, vol. 1. (D. Lehrman, R. Hinde, and E. Shaw, Eds.). New York, Academic Press.

SCHMIDT-KOENIG, K. 1965b. Uber den zeitlichen Ablauf der Anfangsorientierung bei Brieftauben (kurzfassung) Vehr. Dt. Zool. Ges., 28: 407–411.

SIEGEL, S. 1956. Nonparametric statistics. New York, McGraw-Hill.

WALCOTT, C. 1972. The navigation of homing pigeons: Do they use sun navigation? *In* Animal orientation and navigation. Washington, D. C., Natl. Aeronautics and Space Admin.

WALLRAFF, H. G. 1965. Uber das Heimfindevermogen von Brieftauben mit durchtrennten Bogengangen. Z. Vergl. Physiol. 50: 313–330.

WATSON, G. S. 1961. Goodness-of-fit tests on a circle. Biometrika, 48: 109–114.

WATSON, G. S. 1962. Goodness-of-fit tests on circle, II. Biometrika, 49: 57–63.

Division of Biological Sciences, State University of New York at Stony Brook, Stony Brook, New York 11790, and *I. Zool. Institut der Universitat Göttingen, Göttingen, West Germany.* Accepted 20 March 1972.