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Homing in Pigeons with Impaired Vision

(contact lens/frosted/guidance/navigation)

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ABSTRACT In order to test the importance of vision in homing pigeons, their vision was impaired by frosted contact lenses. Pigeons wearing such lenses seemed unable to recognize artificial landmarks at 6-m distance. Nevertheless, most birds homed from distances of 15 km, and some even from 130-km distance. This result indicates that, contrary to common expectation, vision need not play an essential role in homing.

Attempts to explain homing in pigeons have usually focused on vision. A key role has been attributed to the measurement of astronomical data, as well as to the recognition of landmarks (1–4). Recently, a considerable shift away from an emphasis on visual cues has taken place (5, 6), although there have been earlier attempts to explain homing by nonvisual cues (7). However, experiments entailing interference with vision have not been common. We have now succeeded in fitting contact lenses to pigeon eyes (8), and have extended our preliminary homing experiments that used colored, partially painted, and frosted lenses (8). We report here data from flights of experienced birds at distances of 15 and 130 km from their homes.

MATERIALS AND METHODS

All birds were fitted with clear contact lenses several days before each release. Habituation to wearing lenses considerably enhanced the willingness of the birds to fly upon release. On the evening before the release, the clear lenses were replaced with frosted lenses for the experimental birds, while clear lenses were left in the eyes of the control birds. Both groups were transported to the release site immediately before release, and were released in the usual manner (10). Initial orientation and homing performance were used as criteria for homing performance. The presence of lenses was checked upon arrival of each bird. Data from experimental birds that had lost one or both frosted lenses, or the frosted layer of one or both lenses, were discarded.

RESULTS

Fig. 1 gives initial orientation and homing performance of four releases from 15-km west, north, and south of the home loft under sunny conditions, including those published in ref 8. Fig. 2 gives initial orientation and homing performance of three releases from 130-km south, west, and north under sunny conditions. Initial orientation of one release (130-km north) could not be included in Fig. 2, because the distribution of the control birds was random. The original data of this release are, therefore, given in Fig. 3. In this instance initial orientation of experimental birds with frosted lenses was superior to that of controls.

The preliminary finding (8, 9) has been confirmed: frosted lenses had no negative effect on the accuracy of initial orientation of experienced birds, though homing performance clearly was affected. Although many experimental birds did not reach home, a considerable number did so, some even at normal speeds. The number of experimental birds lost is somewhat misleading, inasmuch as several birds got close to the loft, but then missed it by some small distance. Such birds have been found in the vicinity of the loft more or less by chance, but an unknown number were doubtless trapped in corn fields, brushy undergrowth, and the like without being noticed.

The usual behavior of the birds upon release and at the loft was also drastically altered in experimental birds. Upon release, many experimental birds refused to fly, hovered, or

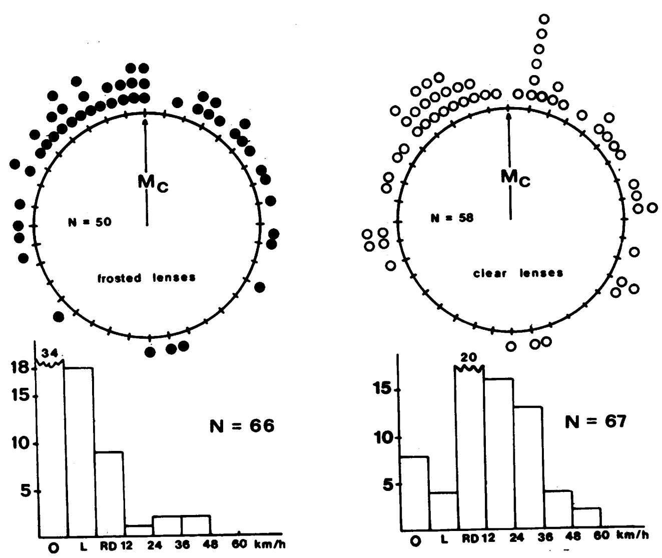

FIG. 1. Initial orientation (*circular diagrams*) and homing performances (*histograms*) of experimental birds (*left*) and controls (*right*) during four releases 15-km west, north, and south of the home loft. Sample size is indicated by N. In the circular diagrams, each spot represents the vanishing direction of one bird when released; the *arrow* M_c, indicates the mean bearings of controls at vanishing. Experimental birds and controls were indistinguishable ($P > 0.1$, Watson test). In the histograms, O refers to birds that failed to return home, L to those that arrived after the day of release, and RD to those returning on the day of release, but at speeds less than 12 km/hr. Faster speeds are given. Experimental and control birds clearly differed in their homing performance, the similarity in initial orientation notwithstanding.

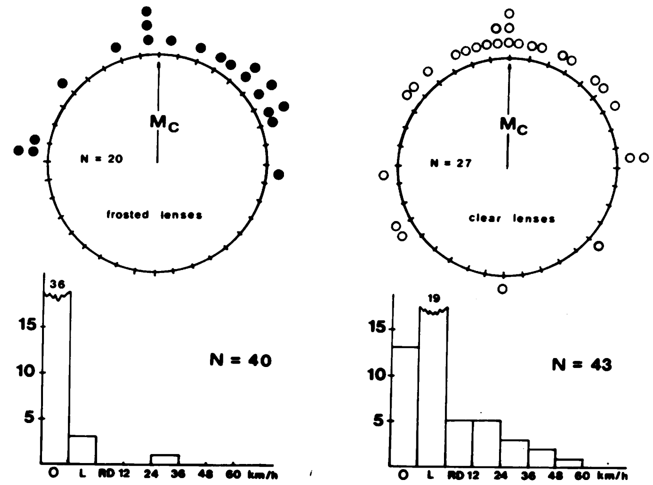

FIG. 2. Initial orientation in two releases 130-km south and west of home, and homing performance in three releases 130-km south, west, and north of home, plotted as in Fig. 1. There is no difference in initial orientation between experimental and control birds ($P > 0.1$; Watson test). For reasons explained in the text, the initial orientation for a third release (130-km north of home) are given in Fig. 3.

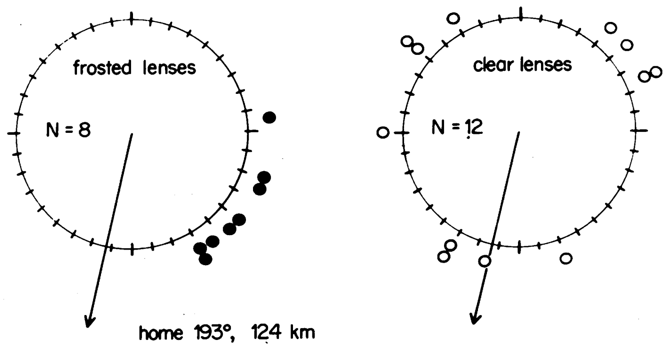

FIG. 3. Initial orientation in a release 130-km north of home, plotted with reference to true north. Symbols as in Fig. 1.

crash-landed nearby; others hit wires, trees, or other obstacles. A certain proportion went high up into the sky and disappeared unusually high above the horizon. All birds that did fly did so in a peculiar way, with the body axis tilted upwards. intermediate between the horizontal axis of normal flight and the upward tilt characteristic of hovering. This expression of "uncertainty" was, obviously, easily recognized by hawks, which were seen repeatedly to prey with ease on such birds. Experimental birds usually arrived at the loft rather high in the sky, cautiously hovering down, a few hitting, most others missing, the loft. The birds could easily be caught by hand. This behavior of the birds clearly demonstrates that their vision was drastically reduced.

In conditioning experiments (9), we determined the degree of visual impairment accomplished by frosted lenses. Pigeons trained to recognize artificial landmarks such as a red pole (5-cm diameter, 130-cm high) were still able to recognize it with frosted lenses at 2-m distance, but not at 6-m distance. The same result was obtained after training to more complex environmental structures, such as the loft entrance. Similarly, a general directional response to distant landmarks, such as a mountain ridge 1-km away, failed as soon as frosted lenses were applied. Under clear skies the sun could still be located, and was used for sun compass purposes with frosted lenses (9). Likewise, a strong spotlight was accepted as an artificial sun and was used for compass reference.

DISCUSSION

These results clearly indicate that vision need not play the central role in navigation that has previously been attributed to it. We cannot exclude that frosted lenses blur the sun to such an extent that the sun cannot be used for measurements as precise as would be required for sun navigation (2, 4). However, it appears less likely that the sun must be used for navigation. We are on firmer ground in concluding that visual landmarks are not used. It appears that visual means may not even be as important as has previously been assumed for pinpointing the loft at the end of a homing flight. This makes the performance of the birds that do find the loft even more astonishing. The current shift in research away from the emphasis on visual cues (5, 6, 11, 12) is thus justified.

More experiments are underway, including tests under heavy cloud cover, with additional magnetic interference, and with inexperienced birds.

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