

MATTERS ARISING

The homing mechanism of pigeons

THE review by Gould¹ misrepresents essential aspects of our knowledge about pigeon navigation. Within the limited space available, I cannot substantiate this for the whole article, but can only enumerate the most drastic shortcomings concerning my own work.

In aviary (palisade) experiments: (1) The related papers²⁻⁴ primarily deal with recoveries which comprise sufficiently large numbers (totalling 691!) to prove statistically significant differences between many of the differently treated pigeon groups. Gould discards all these data and considers only initial bearings, although it has been explained why those data are much less reliable (ref. 4, pp. 215-216). (2) Gould's Fig. 2 is meaningless (i) because of the generally restricted value of those initial bearings, (ii) because the semi-louvred palisade used at first³ cannot be directly compared with the open aviary (ref. 4, p. 216), (iii) because the figure mixes different release and home sites in an unbalanced way, and (iv) because it does not even coincide with the published data^{2,3}.

(3) Gould lumps the data of two 'glass and open lofts' and two 'wood and louvred lofts' irrespectively of the orientation of the corridors open to airflow although just this alignment has been shown to influence the pigeons' behaviour⁴. (4) Gould's site-by-site calculations of angular deviations of experimentals from controls (Table 1) conceal rather than disclose the net homeward orientation, as the relation to home is abolished. (5) "These effects" (of the hybrid aviaries) "are generally interpreted as disrupting the pigeon map sense." I wonder where Gould read this. I stressed the influence of the corridors on the preferred compass direction only, but not on homeward orientation, the part requiring a functioning 'map'.

(6) Real differences in homeward orientation have been found between pigeons from completely open or louvred aviaries and much poorer oriented pigeons from aviaries completely shielded with glass walls⁴. These findings, however, primarily concern the "small proportion" of recoveries (sample sizes 58 and 63) and thus are neglected by Gould. (7) The corridor-aviary results⁴ do not contradict "the olfaction hypothesis", but only a specific version that was published at that time^{5,6}.

Concerning the role of olfaction: (1) Gould writes that in my experiments the nerve-sectioned birds were "slower to home" than untreated pigeons. In fact, they did not home at all⁶. (2) It is well known that anosmic pigeons are not dis-

oriented, but that their preference for a particular compass direction persists⁶⁻⁸. When homing is concerned, however, the level of homeward orientation is crucial^{6,8}, and the parameters extracted by Gould (vector lengths 0.8 and 0.4, average deviation 38°) include no information on that. Homeward components of anosmic pigeons (initial bearings as well as recoveries) are drastically and significantly reduced^{6,9}.

(3) Gould quotes Keeton's mention of a few nasal-tube pigeons that had landed after a short flight¹⁰, but ignores the much more conclusive 75 recoveries of anosmic pigeons (and 61 of controls) at distances ranging from 10 to 700 km reported in my paper⁶. Differences between experimentals and controls in flight directions, yet not in distances, are highly significant. There is no "contrast to the disoriented birds in other" (which?) "experiments who continue gamely flying".

(4) In the nasal-tube experiments of Keeton *et al.*¹¹, "no disorientation was evident". This is true, but appropriate data analysis revealed significant differences between experimentals and controls in initial homeward orientation⁶, and this is the crucial point (see above). (5) Gould confuses the matter when he mixes the primary question of whether olfaction is a substantial component of pigeon homing with the secondary question of how it might be integrated into the navigational system. By considering one specific hypothesis⁷ about this secondary problem, and thus many experiments merely indirectly concerned with olfaction, he creates unjustified doubts also with respect to an affirmative answering of the primary question. After recent extensive discussion of the related problems⁶, this kind of review of the field is obsolete.

The examples selected may warn the reader against trusting this review. Related literature published in the meantime is quoted in ref. 12.

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IN his recent article on the homing mechanism of pigeons, Gould¹ says that when I replicated experiments with anosmic pigeons in Germany² no effect on initial orientation was evident, though homing speed was slower than in controls.

I would like to point out that, in my first series, pigeons made anosmic by inserting nasal tubes were homeward oriented and performed rather well in homing from a familiar site, whereas, when released from an unfamiliar site, they were randomly oriented, unlike the homeward-directed controls (the difference in homeward directedness was significant). To say that the homing speed of experimentals was slower is an overindulgent assessment of their performances; 12 out of 16 birds were lost (against 2 controls out of 18).

In my second series, both controls and experimentals underwent the section of one olfactory nerve and the plugging of one nostril (the contralateral in experimentals, the ipsilateral in controls). Despite this minimization of differences in treatment, homing performances were significantly worse in experimentals, with 61 birds out of 92 lost (against 36 controls out of 90). In this case no differences in initial orientation could be found for the simple reason that bearings of both controls and experimentals were randomly distributed. In this particular respect my experiments were inconclusive, whereas the rest of my results support the olfactory hypothesis.

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GOULD¹ writes that certain results obtained by my colleagues and myself, which support the olfactory hypothesis, "admit of simpler non-olfactory explanations". According to a first, "simpler" explanation, pigeons with nostrils plugged or olfactory nerves cut are slower in homing because of "a generalized, distracting trauma". Besides the fact that anosmia affects not only homing speed but also homing success²⁻⁴, Gould fails to mention other important findings. (1) Homing capacity is strongly reduced in anosmic birds as compared with controls subjected to the same trauma (one nerve cut, one nostril plugged^{5,6}). (2) Birds not subjected to trauma are indeed impaired in homing when prevented from smelling by nasal tubes^{2,5,6}, and disoriented after treatment of the olfactory mucosa with local anaesthetic, provided that smelling during transportation has been prevented⁷. (3)