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RECENT ADVANCES IN STUDIES OF HOMING MECHANISMS

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The ability of certain species to orient homeward from unfamiliar areas has long been studied (Matthews 1968, Emien 1975). Three levels of navigation ability have been defined (Griffin 1955). Type I is simple orientation by means of familiar landmarks (visual or otherwise). Type II is the ability to move in a particular compass direction without reference to landmarks; and Type III, often called true navigation, is the ability to orient homeward (or toward some other goal) from a variety of unfamiliar areas. There is evidence that homing pigeons (Walcott 1974), purple martins (*Progne subis*) (Southern 1959, 1968), the Manx sliearwater *(Puffinus puffinus*) (Mazzeo 1953), the Laysan albatross (*Diomedia immutabilis*) (Kenyon and Rice 1958), and black bears (*Ursus americanus*) (Harger 1970, Alt 1977, Rogers 1984, in preparation a and b) possess Type III navigational ability.

Study of homing mechanisms has concentrated on homing pigeons and has led to the discovery of several surprising sensory abilities in this species. They can detect polarized light (Delius et al. 1976, Kreithen 1978), ultraviolet light (Kreithen 1978, Delius and Emmerton 1978), very low frequency infrasounds (Kreithen 1978), and changes in atmospheric pressure (Delius and Emmerton 1978), but which of these senses might be used to determine the homeward direction is unknown.

Magnetite has been discovered in the heads of homing pigeons (Walcott et al. 1979), dolphins (Zoeger et al. 1981), and man (Baker et al. 1983) and was found in the bodies of bees (Gould et al. 1978) and certain bacteria (Frankel et al. 1979). A current area of concentrated study is determining which vertebrates possess magnetite and use it to orient to the earth's magnetic field. Only the bacteria are known to use magnetite for orientation (Frankel et al. 1979), but the diversity of groups that have magnetite has led to speculation that geomagnetic compass sense may be widespread (Baker et al. 1983). However, even if some species have this sense, the mechanisms of true navigation remain a mystery because a mental map is still needed to use a compass sense.

There is strong evidence that odors are important in the formation of the mental map in homing pigeons (Walraff 1983). Study has concentrated on the role of odors in navigation following reports by Papi et al. (1973) and Benvenuti et al. (1973a, 1973b) that homing pigeons whose sense of smell is experimentally impaired show poor homing success. Papi et al. (1973) proposed that "Pigeons, during their first months of life, would learn to recognize the odors prevailing in the area of the loft, but when the wind blows, they would also receive information about foreign odors from surrounding areas. At the same time they would associate the different foreign odors with the direction from which they come." Followup experiments were conducted in which pigeons were raised in cages with wind deflectors that deceived the birds about wind direction. When released in unfamiliar areas, these pigeons showed predictable errors in orientation (Baldaccini et al. 1975, 1978, Fiaschi et al. 1981). Further experiments to determine whether light (including polarized light), sounds, or infrasounds also were involved in this deflector effect have sometimes shown conflicting results but generally have indicated that odors were of primary importance (Ioale and Benvenuti 1983).

Pigeons commonly return home from hundreds of kilometers away (Walcott 1974), so further experiments were conducted to determine whether olfactory cues also are important at these distances (Ioale et al. 1983). Pigeons released more than about 60 km from home showed poor homing orientation unless they had access to olfactory cues during translocation (Ioale et al. 1983). However, some of the pigeons that were prevented from smelling during translocation oriented homeward (Ioale et al. 1983) as was also reported for completely anosmic pigeons (Walraff 1983). This suggests that pigeons in distant unfamiliar areas use nonolfactory stimuli in addition to olfactory stimuli to determine the homeward direction.

The extent to which black bears use olfactory stimuli for homing has not been tested. However, the homeward orientation of bears that were drugged and unconscious for some or all of their translocation (Harger 1970, Rogers in preparation a) suggests that olfaction during translocation may not be necessary for homing in this species. I thank R. R. Buech, L. D. Mech, and C. Walcott for reviewing the manuscript.

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