Chapter 12
Are Animal Maps Magnetic?

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1. Introduction

A variety of animals travel long distances to relatively small targets (reviewed in Gould, 1982a). For example, honey bees may venture out as far as 15 km from their hive and return safely; vast numbers of monarch butterflies in the eastern United States fly thousands of kilometers to small, isolated mountain forests in Mexico; green sea turtles which hatch on tiny Ascension Island return there as adults years later from feeding grounds thousands of kilometers away; and many species of birds regularly migrate between restricted summer and winter territories, while homing pigeons can successfully return home after being displaced hundreds of kilometers. In each of these examples, the ability to navigate appears to be relatively unaffected by overcasts which block celestial cues, and all raise the question of whether animals have a “map” sense.

A map sense is the ability of an animal to know where it is with respect to its goal. This can be based on information gathered on the journey away from the goal, or familiarity with useful landmarks, or an actual ability to sense location independent of either of these kinds of information. Honey bees provide an excellent example of the simplest sort of map systems. Bees have two strategies for determining where they are. The first is known as route-based navigation: on her outward flight, a forager bee keeps track of the distance and direction of each leg of what may be a very circuitous flight (reviewed in von Frisch, 1967; Gould, 1982a). (As we shall see below, she normally uses the sun’s azimuth as her directional reference, though she has several, hierarchically arranged “backup” systems for use when the sun is unavailable.) At the same time, she factors out the effects of crosswinds on her heading as well as the westward movement of the sun. When she prepares to return home after finding food, she integrates over the various legs of the journey and departs directly for the hive. All the information necessary for her return was gathered on the way out. Consequently, a naive bee passively transported from the hive to a release site will fail to return to her colony. On the other hand, an experienced bee carried to a familiar area will return. Bees appear to construct a mental map of their flight range as they explore the vicinity of the hive in search of food, and call upon that map as needed. Whether this
internal, experience-based map comes to take precedence over the route-based strategy of navigation is not known.

Given that bees can navigate on the basis of familiarity and route-based information, is there any reason to suppose that other animals require anything more? Obviously, familiarity alone cannot explain how sea turtles navigate across the trackless ocean or how pigeons transported in closed cages well out of their normal flight range can home. Monarchs add the further complication that most individuals have never been to the target, and so have no route-based information at all. The issue seems settled in that standard species for investigating vertebrate navigation, the homing pigeon. To use route-based information, a pigeon would need to adopt either (1) an inertial strategy, measuring the accelerations, decelerations, and angular rotations on the way out to compute a net displacement, or (2) a compass strategy, measuring the direction of each leg and estimating distance in some other way.

The inertial strategy is probably ruled out by experiments in which pigeons which were transported after surgical removal or bisection of their semicircular canals—the organs which measure these inertial parameters—homed successfully (Hachet-Souplet, 1911; Huizinger, 1935; Wallraff, 1965, 1972; Keeton, 1974a). Similarly, pigeons and other birds transported under deep anesthesia (Kluijver, 1935; Griffin, 1943; Walcott and Schmidt-Koenig, 1973) or while being constantly rotated (Griffin, 1943; Wallraff, 1980a,b) appear to home normally. The compass alternative seems unlikely as pigeons regularly home after being transported without access to celestial cues (reviewed in Keeton, 1974a) and (usually) when displaced in artificial magnetic fields which would seem at first glance to make information in the earth's magnetic field useless (Keeton, 1974b; Wallraff, 1980a,b). There are, however, two minor holes in the case against route-based navigation in pigeons. First, in most experiments true magnetic direction probably could have been extracted from the strong, artificial background field if the birds wearing the magnets have the appropriate processing circuitry: e.g., if the bird can sense field strength along its body axis, flying in a circle and determining the direction of maximum and minimum field strength would reveal the north–south axis. Second, the lesson from studies of compass orientation (to be mentioned below) is that normally there are at least two alternative systems available so that the elimination of one does not destroy the behavior, because the other automatically takes over. As it happens, no one has excluded both inertial and compass information in the same experiment. As a result, the possibility that pigeons use a pair of route-based strategies cannot be ignored. Nevertheless, the present consensus is strongly in favor of a map sense which is based primarily on information obtained at the release site, and it is the possible sensory basis of this apparent ability which I will explore.

2. The Compass Sense

As mentioned above, one of the most important principles to emerge from the study of navigation is that animals frequently—indeed, usually—have alternative orientation strategies which are used in a preferred order according to what cues are available. For bees, where this hierarchial organization was first discovered, the primary cue is the sun (reviewed in von Frisch, 1967; Gould, 1982a). As a result, contradictory information from other sources will normally be ignored. If the sun is not visible, however, bees automatically switch to using the patterns of polarized UV light in blue sky and so are able to continue to navigate and communicate with good accuracy (reviewed in von Frisch, 1967; see also Brines and Gould, 1979). Under overcast, bees switch to using their memory of the sun's position with respect to prominent landmarks (Dyer and Gould, 1981). Because honey bees continue to perform well under overcast even in the absence of useful land-