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PIGEON HOMING: OBSERVATIONS, EXPERIMENTS AND CONFUSIONS

CHARLES WALCOTT

Laboratory of Ornithology and Section of Neurobiology and Behavior, Cornell University, Ithaca, NY 14850, USA

Summary

Homing pigeons can return from distant, unfamiliar release points. Experienced pigeons can do so even if they are transported anesthetized and deprived of outward journey information. Airplane tracking has shown that they make relatively straight tracks on their homeward journey; therefore, pigeons must have some way of determining the home direction at the release site. Manipulating the pigeon's internal clock causes predictable deviations in their flight direction relative to home. When the sun is not visible, such clock shifts have no effect. This result implies a two-step system: the determination of the home direction and the use of a sun compass to fly in that direction. When pigeons cannot see the sun they use a magnetic compass. The use of compass cues to select and maintain a direction of flight is well understood compared with the uncertainty surrounding the nature of the cues used to determine the home direction when pigeons are released at an unfamiliar site. Because they generally home successfully from any direction and distance from the loft, without requiring information gathered on the outward journey, it seems likely that they use some form of coordinate system. Presumably, a displaced pigeon compares the values of some factor at the release site with its remembered value at the home loft. This factor might be olfactory, it might be some feature of the earth's magnetic field or it might be something else. There is some evidence that pigeons may use several cues and that pigeons raised in different lofts under different environmental conditions may prefer to use one cue over another. I believe that it is this flexible use of multiple cues that has led to so much confusion in experiments on pigeon homing.

Key words: navigation, orientation, homing, pigeon, *Columba livia*, sun compass, magnetic field, olfaction.

Introduction

Homing pigeons released at unfamiliar locations return to their home lofts in most cases. This phenomenon is the basis for a substantial world-wide sport. In the United States, the longest pigeon races involve flights of 1800 km and, because substantial financial rewards accrue to the owner of the fastest pigeon, there is severe selection for those pigeons that home the fastest. Many investigators have used these birds as a model of animal navigation. From an evolutionary point of view, our modern homing pigeons have presumably descended from the wild Mediterranean rock doves. These birds nested on cliffs and foraged for food in nearby fields. Homing probably evolved in the context of returning to the nest site with food for the young. In many ways, a displaced homing pigeon faces a more difficult task than a migratory bird; it has no control and usually little information on the distance or direction of its experimental displacement. Yet, in almost every case, the pigeon finds its way home.

This ability to return home from unfamiliar locations raises the question of what sensory cues pigeons use both to determine the direction towards home and to maintain their flight in that direction. These are two quite distinct processes. In the first, a pigeon must determine the direction to fly in order to reach home. Because, in human terms, this task is something we accomplish by using a map or chart, this position-finding step is often called the ‘map’. The term ‘map’ has unfortunate connotations. It suggests that the pigeon has a spatial representation of the environment. Actually, all the pigeon needs is a direction towards the home loft. Once a direction to fly has been decided upon, a pigeon might use some other cue as a compass to keep on course (Kramer, 1953).

Pigeons can home under a wide variety of conditions. They fly when the sun is visible and when it is not. With training, they will even fly at night. They fly with both head and tail winds, but they land in heavy rain. Indeed, what is remarkable about their homing success is that only a few experimental manipulations, such as anosmia and release at certain locations, prevent a pigeon from reaching home.

Young pigeons seem to make use of information obtained on the outward journey in order to return home (Wiltschko and Wiltschko, 1978). Older pigeons transported to the release site inside sealed metal containers, supplied with bottled air, anesthetized and placed on rotating turntables, all of which should make it hard for them to keep track of their outward journey, still home (Wallraff, 1980; Wallraff *et al.* 1980). This ability implies that these pigeons are able to determine the direction towards home without using information obtained on the outward journey. Since, in contrast to honeybees, pigeons can orient towards home whatever the direction and distance (within 1800 km or so from home) from which they are released, it must be concluded that they can truly 'navigate', i.e. they are able to determine the direction of the home loft from any release point.

Adopting a home loft

Pigeons seem to adopt a home loft at about 6 weeks of age. Before that time, a pigeon will adopt any loft as home; after that, it becomes difficult to train birds to a new loft location. There are reports that the Army Pigeon Corps had a way of training pigeons to constantly changing loft locations, but this was clearly a difficult and laborious procedure (War Department, 1921, 1945). Once a loft location is adopted as home, it seems to last throughout a pigeon's life. I have had birds return to their original loft at Harvard University after being held prisoners in the Lincoln, Massachusetts, loft for 7 years! The process of getting young birds to adopt a new loft seems to be hastened and made more effective by allowing them to fly around the loft, but this activity is not absolutely required. Birds reared in a loft with no external experience can still home, albeit slowly and with poor success (Wallraff, 1979).

Pigeon tracking

One of the most direct approaches to understanding pigeon homing is to follow the birds on their trip home. Hitchcock (1952, 1955) and Griffin (1952) followed flocks visually in an airplane. Talkington (1967) and Graue (1963, 1965) used helicopters, as did Fiaschi *et al.* (1981). Michener and Walcott (1967) followed radio-tagged pigeon in airplanes, and recently Bramanti *et al.* (1988) put individual flight recorders on the backs of pigeons homing in Italy. All the tracks from these experiments show that unmanipulated pigeons fly on relatively straight paths to the home loft. Taken together, the tracks suggest that a displaced pigeon has a clear idea about the direction to its home loft at the outset. And it is this outset orientation that is captured by the 'vanishing direction', the direction in which a pigeon disappears from the view of an observer with binoculars at the release site.

Release site biases

If one looks at the vanishing directions of large groups of pigeons at different sites, rarely do all pigeons choose the same direction; there is scatter in the pigeon's choices. Furthermore, there are differences related to the particular release site which Keeton (1973) called 'release site biases'. As Fig. 1 shows, Cornell pigeons provide several dramatic examples: at Castor Hill, North of Ithaca, the vanishing bearings of Cornell pigeons tend to be deflected to the west. Yet pigeons home normally from the site. At Jersey Hill, 132 km west of Ithaca, Cornell pigeons are disoriented and homing performance is very poor. Releasing pigeons raised in different loft locations at both of these sites shows that their behavior differs between these sites. These results, together with those of Schmidt-Koenig (1963) and many others, indicate that a pigeon's orientation is a function both of its home loft location and of the release site.

Cues used in homing

Pigeons equipped with frosted lenses depriving them of visual landmarks still orient; some even find the loft (Schlichte and Schmidt-Koenig, 1971; Schmidt-Koenig and Walcott, 1978). Clearly, detailed visual information is not essential for navigation. The same is true for birds whose cochleas have been destroyed; orientation was not affected (G. A. Manley, personal commmunication). Appearently, acoustic information is not required either.

Clock-shifts, in which a bird's internal sense of time is altered, do have an effect under sunny conditions. A pigeon with a 6 h clock-shift makes on average a 90° error in its homeward vanishing bearing; the direction of the error depends upon the direction of the shift (Schmidt-Koenig, 1960, 1990; Schmidt-Koenig *et al.* 1991). This error occurs even at very short distances from the lofts, although familiar landmarks are presumably visible (Graue, 1963; Alexander, 1975). It also occurs at both familiar and unfamiliar release points (Fuller *et al.* 1983). Somewhat surprisingly, the exact amount of the error may vary depending on the release point used. There are places around Ithaca, NY, where a 6 h clock-shift results in errors of from less than 40° to more than 110° in the pigeon's vanishing bearings. Many birds with a 6 h clock-shift never home. Birds with smaller clock-shifts exhibit smaller errors and better homing success. Most pigeon researchers report similar results. Keeton (1969) reported that his 6 h clock-shifted pigeons, released under overcast skies, were well oriented towards home. This success implies that the pigeons were not able to see the sun through the clouds and that, furthermore, the sight of the sun was not essential for successful orientation and homing.

Keeton reasoned that if his pigeons were well oriented under overcast they must be using a cue other than the sun compass. He found that pigeons with magnets fastened on their backs were often disoriented when released under overcast (Keeton, 1971; Ioalè, 1984). This effect was very conspicuous at one particular release site (Campbell, NY), but it was much weaker at other release sites. Pigeons equipped with a pair of coils generating a magnetic field of the strength of the Earth's natural magnetic field around their heads had slightly deflected vanishing bearings under sun. Although the effect was only 10–20° and statistically not significant for any one release, it was consistent (Walcott, 1977). When the sun was not visible, birds wearing coils with one magnetic polarity (SUP; the south-seeking needle of a compass placed between the coils pointing up, towards the pigeon's head coil) vanished towards home, whereas birds with coils of the opposite polarity (NUP) vanished in the opposite direction (Walcott and Green, 1974; Visalberghi and Alleva, 1979). The behavior of a pigeon wearing a set of head coils depends dramatically on the

Fig. 1. Vanishing bearings of unmanipulated Cornell pigeons released at various locations around their home loft in Ithaca, New York. Each symbol represents the direction of the mean vector of releases on 1 day. The length of the symbol is proportional to the degree of clumping of each day's vanishing bearings. At most locations, the vanishing bearings were directed towards the home loft (filled circle near center). But near Castor Hill on the Tug Hill Plateau (A, 160 km northnortheast of Ithaca) pigeons tended to fly west rather than south. At Jersey Hill Fire Tower (B, 132 km west of Ithaca), Cornell pigeons vanished randomly.

visibility of the sun. Under a sunny sky, the coils, whatever their polarity, only deflect the pigeon's vanishing bearings by a few degrees. If a pigeon wearing an NUP coil starts its homeward journey under overcast, it will head away from the release point in the direction away from home. Should the sun appear, even if only momentarily, through a hole in the clouds, it will reverse course and head directly for home. Whereas the behavior of birds with magnets seems to depend somewhat upon where they are released, the vanishing bearings of birds with coils seem to be more consistent. Why this should be so is unclear.

Map and compass

Both clock-shifts and magnetic head coils seem to deflect the pigeon's vanishing bearings with respect to the home direction. This observation provides support for Kramer's idea that pigeon homing is a two-step process: a 'map' to determine the direction towards home and a compass to guide the bird in that direction (Kramer, 1953). The most likely interpretation of the clock-shift experiments is that they have introduced an error into the sun compass system, but since the pigeon flies off at an angle with respect to the home direction, the bird still obviously knows the direction towards home. But a pigeon headed towards home with a 6 h clock-shift (and hence a 90 ° deflection) might be able to correct its course after a period of flight. We tracked a small number of such birds by airplane and, although their tracks are somewhat fragmentary, it appears that they approach home in a converging spiral. This must mean that they continue to update the direction towards home as they fly, each time with the same 90 ° error. If the error were greater than 90 °, the spiral would never converge on home. If it were less, as in a 2 h shift, convergence would be rapid. Maybe this is why many 2 h shifted birds home more successfully than birds with 6 h shifts. By looking at the shape of the spiral, one can calculate that birds with 6 h shifts must re-compute the direction towards home roughly every 15–30 min.

Map cues

In Italy and Germany, a long series of ingenious experiments has provided evidence that olfactory cues are important in pigeon homing (for reviews, see Wallraff, 1990; Papi, 1986, 1989, 1991). Birds with their olfactory nerves sectioned neither orient nor home from unfamiliar sites. Pigeons whose exposure to natural air flow has been manipulated by deflector lofts or by tunnels show the predicted deflection of their vanishing directions. Birds transported long distances do not orient unless they are allowed to sample the natural air on the outward journey; filtering the air through charcoal eliminates the pigeons' ability to orient (Wallraff and Foà, 1981). These and many other observations make a convincing case that pigeons make some use of olfactory information in their orientation.

The Earth's magnetic field is another potential 'map' cue. The field varies in both strength and direction over the Earth's surface. A pigeon that was able to measure tiny differences in either angle or strength of the field could, at least in theory, tell where it was on the surface of the Earth. Wiltschko and Wiltschko (1988) and Able (1994) have written excellent reviews on this subject. Infrasound has also been suggested as a potential map cue. Pigeons are sensitive to very low-frequency sounds down to 0.1 Hz. Perhaps they could use sources of such sounds as acoustic guideposts (Yodlowski *et al.* 1977; Kreithen and Quine, 1979). Pigeons can respond to polarized light patterns (Kreithen and Keeton, 1974); they can also detect ultraviolet light (Kreithen and Eisner, 1978). What role these abilities might play in their orientation is completely unclear.

Multiplicity and interaction among cues

The orientation of pigeons exposed either to clock-shifts or to magnetic manipulations suggests that the birds know the direction to home and that the experimental manipulations are deflecting their vanishing bearings in relation to this home direction. Clock-shifts and magnetic coils cause the pigeons to select a wrong compass direction, but the errors that they make show that the treated birds nevertheless possess information on the direction of their home loft. If this is so, then what is the nature of the cues that provide information on the home direction?

Let us begin by first excluding several cues. Finding the correct home direction does not require a view of the sun. Pigeons select the home direction in the presence of both Earth-strength and weaker static and varying magnetic fields (Lednor and Walcott, 1983). This performance also does not require acoustic cues (G. Manley, personal communication). The results of three sets of experiments, described below, suggest that determining the home direction is based on redundant cues, as in the case of the compass system.

Pigeons raised in our lofts at Cornell in Ithaca, NY, are disoriented and few home when released at Jersey Hill Fire Tower, which is located 132 km west of Ithaca. Birds raised in other lofts, even one as close as 18 km to our Cornell lofts, are well oriented at Jersey Hill. Cornell-born pigeons raised in other lofts are well oriented, pigeons born in other lofts and raised at Cornell are disoriented. Clearly, being raised at the Cornell pigeon lofts interferes with orientation at Jersey Hill (Walcott and Brown, 1989).

In Frankfurt, Germany, pigeons raised in a loft in the courtyard of the Zoological Institute are about equally well oriented whether or not they are made anosmic. Their siblings raised on the roof of the four-storey building with access to the free winds become disoriented when made anosmic. Here, it appears that the cues that the birds use may well depend upon the circumstances of their rearing (Wiltschko *et al.* 1989; Wiltschko and Wiltschko, 1989).

In Lincoln, Massachusetts, USA, pigeons raised in one loft were disoriented when released at a magnetic anomaly. Their siblings raised in a loft only 2.5 km away were well-oriented at the same anomaly. Since both releases took place under sunny skies, when a sun compass was available, we are tempted to suggest that one group of birds might have been using magnetic information to find their homeward direction while their siblings from the other loft were using some other cue (Walcott, 1992).

Pigeon behavior differs at familiar and unfamiliar sites. For example, pigeons released at magnetic anomalies are better oriented on their second release at the same anomaly. Yet experience at other anomalies does not help their performance at a test anomaly (Lednor and Walcott, 1988). Experienced pigeons made anosmic by olfactory nerve section or anesthetics are disoriented at unfamiliar sites and their homing is poor, whereas at familiar sites, the same birds both orient and home (Streng and Wallraff, 1992). Birds that have been raised in lofts with a view of the landscape home faster when they are allowed to view the landscape around the release site before beginning their flight home (Braithwaite and Newman, 1994; Braithwaite and Guilford, 1995). Clearly the birds are learning something about the release site itself. In contrast, pigeons released at Jersey Hill show no great improvement in either their orientation or homing success on subsequent releases.

Pigeons released at magnetic anomalies, once outside the magnetically disturbed area, turn and head for home. Much the same is true of pigeons released at Castor Hill. These birds headed off on an incorrect course that they later corrected. In contrast, birds tracked from Jersey Hill continued steadfastly on their incorrect course, with only a small percentage correcting it towards home (B. Moore and R. Madden, personal communication). What is especially surprising about these Cornell birds released at Jersey Hill is that they often flew over

Table 1. *Potential cues that might be used by homing pigeons in returning to their lofts*

Potential cue	Compass or map	Geographic scale	Evidence	Certainty	Review
Sun azimuth	Compass	Hemisphere	Clock-shift	High	Schmidt-Koenig *et al.* (1991)
Sun position	Map	?	None	Out	Schmidt-Koenig (1972); Walcott (1972)
Odor, mosaic	Map	Local	Detour Site simulation	Medium	Papi (1991)
Odor, gradient	Map	10^3 km	Long-distance	Medium	Wallraff (1990); Waldvogel (1989)
Magnetic field	Compass	World	Magnets	High	Wiltschko and Wiltschko (1988)
Magnetic field	Map	?	Anomalies	Medium	Able (1994)
Visual landmarks	?	Local	Frosted lenses	High	Schlichte (1973); Braithwaite and Guilford (1995)
Infrasound	Map	Long	None	?	Yodlowski *et al.* (1977); Quine (1982)
Polarized light	Compass	Hemisphere	None	Low	Waldvogel (1990)

Compass or map refers to whether a cue is likely to be used for direction finding (compass) or position finding (map). Geographic scale is the size of the region in which the cue is likely to be useful. Evidence is main experimental evidence, and certainty is the degree to which there is general agreement that the cue is used. Review is the most current or most useful reference to the literature.

areas from where, had they been released there in the first place, they would have homed well. This is also true of clock-shifted birds; airplane tracking shows that they continue on their shifted course even over presumably familiar terrain. The difference is that clock-shifted pigeons seem to correct their courses, whereas birds released at Jersey Hill do not. This difference implies that the clock-shifted birds continually update their knowledge of the home position whereas birds released at Jersey Hill seem to have no idea where home is located. Why Cornell birds have such problems at Jersey Hill is completely mysterious.

If the map is based on the comparison of some factor at the release site with its remembered value at the home loft, then there seem to be two categories of places. First, there are locations where this comparison is agreed upon by all birds from a specific loft and where they predominantly choose some direction other than home. At Castor Hill, on the Tug Hill plateau, Cornell birds are all agreed about the direction to fly even though it is not the correct direction to home. Here, the comparison of some mysterious cues leads to a consensus, even if it is wrong (Keeton, 1973). In the second category are release sites where the comparison does not yield useful information. Each pigeon comes to a different conclusion about the direction towards home, and the pigeons vanish at random. The releases at magnetic anomalies, as well as the Jersey Hill releases, belong to this second category. They differ, however, in that Cornell birds released at Jersey Hill never correct their courses and few home successfully, whereas birds from magnetic anomalies correct their courses and home normally.

A further interesting observation was made when pigeons from our old Lincoln, Massachusetts, lofts that were disoriented by magnetic anomalies were released at magnetically normal sites but had to fly over a magnetic anomaly on their way home. Generally, such pigeons flew on normal, straight homeward courses. Occasionally, a pigeon gave evidence of being disoriented by the anomaly (Fig. 6a in Gould, 1982). This exception provides further evidence that pigeons determine the direction to home at the release site and only occasionally check positional information on their homeward trip.

All of these experiments suggest that the 'map' or home vector sense seems to rely on a comparison of some factor which may depend on loft location, release site and, presumably, available cues. Ganzhorn's (1989, 1992) analysis of the various release points for Cornell birds divides them into various clusters according to the vanishing bearings of the birds. Furthermore, he points out that magnetic manipulations have an effect at some release sites and olfactory manipulations at others. Clearly, the pigeons' behavior depends on multiple cues. Which cues they use seems to be a function of both the loft and its location as well as of the release site (Schmidt-Koenig and Ganzhorn, 1991). Table 1 summarizes the different potential cues.

Much of the confusion in the pigeon homing story may well result from the differences among various lofts and release sites. Even such well-known and agreed upon manipulations as clock shifts have different effects at different release sites. Given this degree of variability, it should be no surprise that different investigators obtain different results with pigeons living in different areas!

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