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REVIEW

Cues indicating location in pigeon navigation

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Abstract Domesticated Rock Pigeons (*Columba livia f. domestica*) have been selected for returning home after being displaced. They appear to use many of the physical cue sources available in the natural environment for Map-and-Compass navigation. Two compass mechanisms that have been well documented in pigeons are a time-compensated sun compass and a magnetic inclination compass. Location-finding, or map, mechanisms have been more elusive. Visual landmarks, magnetic fields, odors, gravity and now also infrasound have been proposed as sources of information on location. Even in highly familiar locations, pigeons appear to neither use nor need landmarks and can even return to the loft while wearing frosted lenses. Direct and indirect evidence indicates magnetic field information influences pigeon navigation in ways that are consistent with magnetic map components. The role of odors is unclear; it might be motivational in nature rather than navigational. The influence of gravity must be further analyzed. Experiments with infrasound have been interpreted in the sense that they provide information on the home direction, but this hypothesis is inconsistent with the Map-and-Compass Model. All these factors appear to be components of a multifactorial system, with the pigeons being opportunistic, preferring those cues that prove most suitable in their home region. This has made understanding the roles of individual cues challenging.

Keywords Visual landmarks · Magnetic field · Olfaction · Gravity · Infrasound

Introduction

Domesticated Rock Pigeons (*Columba livia* f. *domestica*), also known as homing pigeons, have been used for studies of animal navigation for decades because they are domesticated, can be raised in large numbers, and almost always return home despite the experimental manipulations. Songbirds by comparison are widely distributed during the breeding season, much harder to capture in large numbers, and might abandon their breeding site after capture, thus making them more difficult to study. Consequently, much of our knowledge about avian navigation is based on the study of pigeon homing. There are recent, extensive reviews on avian navigation (Wallraff 2005a; Wiltschko and Wiltschko 2009, 2015; Deutschlander and Beason 2014; Holland 2014), and the reader is encouraged to pursue those for more detailed information. The purpose of this review is to place the paper by Hagstrum and Manley (2015), published in this issue of the *Journal of Comparative Physiology A*, in the context of research on pigeon navigation cues.

Avian navigation is usually considered to be based on the Map-and-Compass Model proposed by Kramer (1953, 1957). Proposed alternate mechanisms include piloting, i.e., following a sequence of landmarks from one to the next (Griffin 1952), gradient following toward the value of the goal and goal-emanating cues that provide a direction toward the goal, but not a compass direction (for review, see Deutschlander and Beason 2014). The Map-and-Compass Model is based on a map that provides information on the birds' location and the compass direction to its goal and

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a compass cue that provides information where this direction lies. The map component usually is considered to have (at least) two independent, non-parallel gradients to provide location coordinates. The gradients do not need to be perpendicular, but should also not be too acute (see Benhamou 2003). They need not be from the same source but their variations should be independent of one another. Two direction-finding or compass mechanisms that fit Kramer's (1953, 1957) Map-and-Compass Model have been well documented in pigeons: sun compass and magnetic compass, and their way of functioning is fairly well understood. By contrast, the location-determining or map component has been more difficult to elucidate. Pigeons have proven to be opportunistic in their use of the environmental cues that are available and that they can detect (Walcott 2005). Their use of multiple sources of information has made it difficult to evaluate the roles of specific sources of information. This has resulted in controversies and unresolved issues regarding the roles of individual sources of information in pigeon navigation. The present mini-review is devoted to the mechanisms and cues involved in the first step of avian navigation that allows pigeons to determine their location and the course to the goal.

Sensory perception

Visual landmarks

It seems intuitive to humans that displaced pigeons could use visual landmarks to determine their locations at a familiar release site or to guide them along a familiar route to their home loft, but this does not seem to be the case (Wallraff 2005a, b). Pigeons use landmarks around the familiar area of their loft but apparently not at greater distances, not even at very familiar sites (Holland 2003). Pigeons fitted with frosted lenses and released remotely were able to fly in the direction of their lofts and get within 1 km (Schmidt-Koenig and Walcott 1978; Benvenuti and Fiaschi 1983); in some cases, they were even able to enter the loft (Schlichte 1973). A variety of studies indicates that pigeons released within view of distinctive visual landmarks near their loft do not seem to use those landmarks as beacons to select their direction of travel. The birds appear to know their locations relative to the loft, but they depart nevertheless from the release site with a deflection predicted by the experimental manipulation of their sun compass (e.g., Keeton 1974; Wiltschko et al. 2005; Biro et al. 2007; Armstrong et al. 2013). On the other hand, pigeons do use their vision to guide their flight path on a local scale and in the vicinity of home (Wallraff 2005a; Guilford and Biro 2014). It appears possible that they do not rely more strongly on visual cues while homing because their visual fields are organized very differently from our own (Martin 2014); in particular, their lower visual field myopia (Fitzke et al. 1985; Hodos and Erichson 1990) might make it difficult to distinguish and identify individual features.

The geomagnetic field

Wiltschko and Wiltschko (2013, 2014) recently reviewed the proposed mechanisms birds might use to sense the Earth's magnetic field. The two mechanisms that have received the most experimental and theoretical support are (1) the use of a radical pair mechanism involving a photopigment and (2) the use of a magnetic material, such as magnetite. The two mechanisms have been suggested to serve different functions, with the radical pair mechanism providing directional information for the magnetic compass and the magnetite-based mechanism information on magnetic intensity used as a magnetic component of the map (Beason and Semm 1987; Wiltschko and Wiltschko 2007). Here, we focus on the latter function.

Indirect support for pigeons using magnetic information in their map comes from experiments in which birds were released within or near magnetic anomalies (Walcott 1978, 1992, 2005; Kiepenheuer 1982; Dennis et al. 2007; Wiltschko et al. 2009; Schiffner et al. 2011). The magnetic anomalies were characterized by steep gradients in the ambient magnetic field, typically caused by ancient volcanism and iron deposits that generate local fields with gradient directions different from the overall gradient of the region. Pigeons released within strong anomalies typically showed greater scatter in direction up to random and took longer to return home. Once free of the influence of the anomaly, New England birds turned toward home (Walcott 1978); in Germany, birds corrected their course even while still in the anomaly, probably switching to non-magnetic cues (Schiffner et al. 2011).

A magnetic map has also been tested in cage studies with migratory birds that were exposed to fields simulating sites within and beyond their natural migration range. In the former case, birds continued in their migratory direction; in the latter case, they went random (Henshaw et al. 2010; Deutschlander et al. 2012).

As magnetoreceptor mechanism for this magnetic information, deposits of magnetite found in the in ethmoid region in pigeons were proposed (Walcott et al. 1979). Magnetite (Fe_3O_4) is the most common magnetic mineral on Earth and has the strongest magnetic moment of any naturally occurring magnetic material. Deposits of magnetite were also reported in the skin of the upper beak (Fleissner et al. 2007; Tian et al. 2006) in pigeons and several migratory species (Falkenberg et al. 2010). These latter deposits were later claimed to be contained within macrophages not magnetoreceptors (Treiber et al. 2012), although electrophysiological and behavioral evidence strongly supports the existence of magnetite-based receptors in the beak and the ethmoid region (see Wiltschko and Wiltschko 2013).

Pigeons that were treated to a magnetic pulse strong enough to remagnetize magnetite and too rapid for the particles to rotate produced a deflection in the homeward orientation of the birds (Beason et al. 1997). Because the birds were not disoriented, i.e., they were significantly oriented as a group but in a direction other than homeward, their compass systems appeared to function normally. Instead they acted as if they were transported to another location and released. Thus, the authors concluded that the treatment changed the way the magnetic receptors transduced information about location. Similar experiments with migrants produced corresponding results (Holland and Helms 2013).

Electrophysiological recordings from the ophthalmic nerve and trigeminal ganglion in a songbird revealed the presence of spontaneously active units that respond to changes in the magnetic field (Beason and Semm 1987; Semm and Beason 1990). These findings were confirmed by neuroanatomical studies with c-Fos and ZENK, revealing neuronal activity in the ophthalmic tract and the trigeminal brain stem after exposing pigeons and a migratory species to a constantly changing magnetic field (Heyers et al. 2010; Lefeld et al. 2014). Mora and coworkers (2004) conditioned pigeons to distinguish a large change in magnetic field intensity (and resulting change in direction) around them. This ability disappeared when the ophthalmic branch of the trigeminal nerve was transected. These results, together with cage studies where ophthalmic nerve section (Beason and Semm 1996) or local anesthesia of the upper beak of migrants abolished the effect of a strong magnetic pulse (Wiltschko et al. 2009b), support the idea that receptors in the rostral and ethmoidal area of the pigeon, innervated by the ophthalmic nerve, provide information on the ambient magnetic field. Because the magnetic compass was unaffected—the birds continued in their migratory direction—this information was interpreted as information on location, i.e., map information, for pigeons and songbirds. Responses of pigeons to small fluctuations in the geomagnetic field suggest a sensitivity in the range of 10–20 nT (Keeton et al. 1974; Schiffner and Wiltschko 2011).

Odors

The role of airborne chemical cues in pigeon navigation has been long debated since Papi and associates first put forth experimental evidence that airborne odors influence pigeon navigation (Papi et al. 1972, 1978a). Other researchers reported conflicting results when replicating the experiments (Papi et al. 1978b). The viewpoints of the debate have been reviewed in depth elsewhere (Papi 2001; Wallraff 2004, 2005a, 2014; Phillips and Jorge 2014). As research on the topic progressed, the proposed navigation mechanism was that the pigeons identified the direction toward home by comparing the odors at the release site with the direction the wind was blowing when those odors were smelled at home. Thus, the spatial distribution of odors in the environment provided the compass course to the home loft: an olfactory map. A proposed strategy was that experienced pigeons used a gradient map of odors to determine their location with respect to home and their home direction (Papi 1986). Later, it was also considered that pigeons might return home by following increasing or decreasing concentrations of specific odors (Wallraff 2005a). Results from release experiments by other researchers challenged the use of odors by pigeons for navigating (Keeton and Brown 1976; Keeton et al. 1977). Wiltschko coworkers (1987a, b), suggested that pigeons exposed to reliable cues in their loft might use olfactory cues at the release site; those that only had unreliable cues, caused by wind eddies around buildings, did not.

In a series of releases, experienced pigeons were exposed to bottled air during transport and had access to natural odors only at a location opposite to the release sites (Experimental birds), or only at the true release site (Control birds). This caused the Control birds to depart directly toward home, whereas the experimental birds departed in the opposite direction (Benvenuti and Wallraff 1985). Subsequent manipulations of the air en route and at the stopover site and release site were similar to those of the original experiments and consistent with the idea that pigeons obtain location or map information from natural odors (Wallraff 2004, 2005a).

Jorge et al. (2010) replicated the experiments in which pigeons were exposed to natural air or filtered air with results similar to Benvenuti and Wallraff (1985) and confirmed the importance of odors in pigeon homing. However, the exception to the pattern predicted by the olfactory map model was a group of birds exposed to artificial odors at the site opposite to the release site rather than to the natural odors of that site. Those birds could not have received any map information by natural odors during their treatment, but they responded as if they had received navigational information from the opposite site. This finding led Jorge et al. (2010) to conclude that odors served as a motivation cue rather than navigation cue (if they were navigational cues the birds should have been disoriented), promoting the processing of non-odorous navigational cues. The results of other behavioral and neuronal studies are consistent with the idea that odors are motivational in nature rather than navigational (Jorge et al. 2009, 2014, but see Gagliardo et al. 2011). These results indicate that at least some "olfactory navigation" effects may be motivational rather than navigational.

Gravity

Gravity has been discussed as a navigational cue, but its possible role is unclear. First experiments in a gravitational anomaly were negative in the sense that the pigeons' behavior seemed unaffected (Lednor and Walcott 1984), but Dornfeld (1991) reported that gravity anomalies had some effect, occasionally leading to poor initial orientation. Recently, Blaser et al. (2013, 2014) reported increased scatter, disoriented behavior and losses in and near gravity anomalies, which they attributed to the altered gravity conditions. They proposed a "gravity vector hypothesis", with gravity as a navigational factor. However, this hypothesis requires extremely precise measurements and unrealistic storage conditions and is incompatible with the Map-and-Compass Model.

Sounds

Griffin and Hopkins (1976) reported that birds aloft can hear many natural and anthropogenic sounds emanating from the ground long distances away. Natural sounds include waves on a shore, wind, animal vocalizations, etc. (Mukhin et al. 2008). Hearing a coastline would be as effective as seeing it and would have a greater range, especially in the range of infrasound frequencies (<20 Hz) (Arrowsmith and Hedlin 2005). Lower frequency sounds, especially infrasound, travel farther in the atmosphere with less attenuation compared to higher frequencies, because atmospheric attenuation is a function of the square of the frequency (Bedard and Georges 2000). This makes infrasound an attractive mechanism to consider as a source of location information for long-distance navigation. Pigeons have demonstrated behavioral and neural sensitivity to frequencies as low as 0.05 Hz (Kreithen and Quine 1979; Schermuly and Klinke 1990).

The direction of an auditory sound source can be determined by comparing the differences in phase or sound intensity between the ears. The long wavelength (100–10,000 m) of low-frequency sound, particularly infrasound, and the small spacing of a pigeon's ears (cm) make detecting interaural differences in timing impossible. In addition, at infrasound wavelengths, the sound refracts around objects that are much smaller than the wavelength (such as a bird's head), negating the ability to discern differences in sound intensity. One approach to determine the direction to an infrasound source might be to determine the Doppler shift or intensity changes as a bird flies fly around, as pigeons often do when taking off (Quine and Kreithen 1981; Hagstrum 2000). Thus, a bird could use a single source of infrasound as a landmark or a reference point.

Hagstrum (2013) suggested that the flying around at the release site may be used to deduce the direction to the home loft directly if the bird could detect the infrasound originating at the loft. He modeled atmospheric propagation of infrasound from the late W. Keeton's Cornell University pigeon loft to selected release sites where the orientation behavior had proven enigmatic. At one of these sites, the Cornell pigeons were always disoriented, whereas at the other they showed a large deflection from a direct path to the home loft. Based on data collected by Keeton and his colleagues, Hagstrum (2013) showed a correlation between the model's predictions of atmospheric infrasound propagation and the ability of the pigeons to orient toward home. On dates, when the atmospheric model-predicted infrasound from the loft was available at the release site, the pigeons were oriented homeward or at a predicted angle way from home. When the model-predicted that infrasound would be ducted upwards and not available at the release site, the birds were disoriented. Hagstrum (2013) concluded that a site where Cornell pigeons were always disoriented, Jersey Hill, was shadowed from the home loft by persistent atmospheric conditions. Note that this model of navigation by infrasound is not compatible with the Map-and-Compass Model; infrasound is not considered a map factor indicating the home direction, but rather something related to a beacon guiding the birds without a compass.

In their paper published in the present issue, Hagstrum and Manley (2015) analyzed data from other sites near Keeton's loft to test whether orientation and homing performance of pigeons deafened by removal of their cochleae and lagenae was impaired. The results are rather inhomogeneous: for most releases the Control birds were better homeward oriented than the deafened birds, but there were also cases where the opposite was true. For some releases in which the Control birds were not well oriented toward home, atmospheric propagation models seemed to indicate infrasound frequencies were refracted upwards and would not have been detectable on the ground. In cases not explained by the daily atmospheric models, the authors inferred a lack of infrasound cues at the release site caused by atmospheric shadowing. Consequently, the acoustic propagation models can explain at least some of the behavioral responses at Keeton's loft, but not all of them.

Whether the acoustic navigation model can account for pigeon homing across the hundreds of kilometers used in pigeon races is a question yet to be answered. Yet the model, as it stands now, has other serious weaknesses: (1) It does not explain convincingly the use of the sun compass as demonstrated by numerous clock-shift experiments. (2) The assumption that untreated and operated birds in principle use different strategies is highly speculative and unsupported. If the operated birds generally use route-reversal, why are there cases where they are poorly oriented or disoriented? (3) Birds need to fly around to detect the direction of infrasound. However, already Kramer (1959) reported that pigeons are oriented in the direction in which they later vanish 10 s after release, i.e., after flying about 150 m. Experiments releasing pigeons from a cage clearly showed that they are normally already aware of their later vanishing direction even before they fly (Chelazzi and Pardi 1972; Kowalski 1994; Mazzotto et al. 1999). This excludes the sole use of infrasound cues that Hagstrum and Manley (2015) seem to promote; it seems possible, however, that infrasonic information is later included in the navigational process. (4) How acoustic cues are integrated with the others cues whose involvement is documented by numerous experimental manipulations is a completely open question which the authors not even attempt to answer.

Conclusions

There is strong evidence that the navigation of Domestic Pigeons is based on the Map-and-Compass Model: hundreds of examples demonstrate the deflection caused by manipulations of the time-compensated sun compass. This, in turn, means that the birds derive their home direction as a compass course probably from the scalar values of gradient fields, comparing the local values at the release site with those at the home site with the help of their map, a mental representation of how the respective gradient fields are distributed in their home region. Such a procedure largely excludes strategies like directly following gradients of, e.g., magnetic intensity or odors, but also the exclusive use of cues like infrasound that do not indicate compass courses.

While the compass mechanisms are well understood, candidate cues for the “map” part of the navigation system are less clear-cut. Experience has shown us that there is no single source of navigation information for pigeons, but that the map is a multifactorial system (Walcott 2005), and here, Hagstrum and Manley (2015) introduce an important new component. The map, i.e., the pigeons’ mental representation of the navigational cues and their spatial distribution, is learned. Young pigeons acquire the first map information as soon as they begin flying around their loft; they explore the home area and the lay of the land. Doing this, they familiarize themselves with the potential navigational factors in their home region. Pigeon seem to be adaptive in exploiting the sources of navigation information that are available in the environment, relying on those that prove most suitable and most reliable. This may lead to the phenomenon that pigeons in different regions prefer different cues—the findings in one region cannot necessarily be generalized, and the same treatment does not necessarily have the same effect in different countries (see, e.g., Wiltschko et al. 1986 for an example). Infrasound signals may be a helpful cue in the Ithaca region with its topography of steep cliffs and deep gorges, but may be completely unsuitable in other regions with different sound profiles. The same may be true for other cues—we must expect that the specific map cues used by pigeons directly reflect the situation in their home region. This has the advantage that the navigational system is optimally adapted to the region where it is used, but makes the analysis of the navigational cues not easier.

Do Rock Pigeons make a good model species to study navigation of migrating songbirds, shorebirds, waterfowl, and other species? The implicit answer has been “probably yes”. There are many parallels between pigeons and other birds (see Wiltschko and Wiltschko 2015), a most prominent one being that at Castor Hill, where Ithaca pigeons show a strong deflection from the home direction that Hagstrum (2011) attributed to a deflection of infrasonic cues—Bank Swallows (*Riparia riparia*) from a colony near the loft show a very similar deflection (Keeton 1973).

Are there any unknown sources of positional information in the environment? This is unclear. Our difficulty in understanding the “map” component of avian navigation is likely due to other problems: the lack of understanding of the sensory physiology of the receptors involved, how the bird interprets the sensory information, or how the information from multiple sensors is integrated.

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