



Navigation mechanisms in homing pigeons: integrating magnetoreception, olfaction, solar and visual cues

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Abstract. Homing pigeons (*Columba livia*) represent a cornerstone model in the study of animal navigation, demonstrating an exceptional ability to integrate multiple environmental cues across spatial scales. This mini-review synthesizes current knowledge on the multimodal navigation system of homing pigeons, focusing on the interaction between magnetoreception, olfaction, solar orientation, and visual-landmark guidance. The classical map-and-compass framework remains fundamental, with olfactory gradients playing a primary role in large-scale positional determination, while compass systems, particularly the time-compensated sun compass, provide directional information. Visual cues and landmark-based navigation dominate in familiar territories and during the final homing phase, supported by hippocampal spatial processing. Magnetoreception, although experimentally demonstrable and likely mediated via trigeminal pathways, appears to play a limited or context-dependent role in true navigation, functioning mainly as a supplementary compass cue under specific environmental conditions. Evidence from behavioral experiments, GPS tracking, and neurobiological studies supports a flexible, redundant system in which multiple cues are dynamically weighted depending on context. This integrative perspective highlights the adaptive significance of multisensory processing in avian navigation and underscores the importance of considering ecological validity when interpreting experimental findings.

Key Words: homing pigeons, navigation, olfactory map, magnetoreception, sun compass, visual landmarks, hippocampus, spatial orientation, multisensory integration, avian navigation.

Introduction. Pigeons (*Columba livia*) are widely regarded as model organisms for investigating spatial orientation and navigation, owing to their remarkable homing abilities and robust flight performance (Ionescu & Oroian 2015; Ionescu et al 2015; Zan et al 2023; Zhang et al 2023; Zhang et al 2024). Their capacity to integrate multimodal environmental cues has made them a central system for studying the mechanisms underlying long-distance navigation and aerial movement.

Homing pigeons constitute the classic neuroethological model for avian navigation, in which a multi-component, hierarchically organized system integrates positional ("map") and directional ("compass") information over a wide range of spatial scales (Keeton 1974; Wallraff 2001; Wiltschko & Wiltschko 2017). Contemporary work, supported by GPS and neurophysiological approaches, shows that olfactory, solar, magnetic and visual-landmark cues interact in a flexible, redundant fashion rather than through any single dominant mechanism (Gagliardo & Bingman 2024; Walcott 2005; Wallraff 2001; Biro et al 2007).

The aim of this mini-review is to provide an integrative and up-to-date synthesis of the principal navigation mechanisms in homing pigeons, with a particular emphasis on how magnetoreception, olfactory cues, solar orientation, and visual information interact within a unified functional framework. Specifically, the review seeks to (i) clarify the relative contributions of each sensory modality to the "map" and "compass" components

of navigation, (ii) evaluate the extent to which magnetoreception contributes to large-scale spatial orientation compared to other cues, and (iii) highlight the neuroethological basis of cue integration across different spatial contexts. By consolidating behavioral, ecological, and neurobiological evidence, this review aims to refine current understanding of multimodal navigation and identify key areas of ongoing debate and future research directions.

Map and Compass: Functional Architecture. Kramer’s map-compass framework remains central: a position-finding “map” is combined with one or more compass systems, notably a time-compensated sun compass and, under certain conditions, a geomagnetic compass (Keeton 1974; Wallraff 1988; Walcott 2005; Wiltschko & Wiltschko 2017). Classic clock-shift experiments, in both pigeons and wild seabirds, demonstrate robust use of a solar compass whose azimuth is corrected using the circadian clock (Walcott 2005; Padget et al 2018; Armstrong et al 2013). Within familiar areas, compass information continues to influence flight trajectories even when birds are flying along well-learned landmark routes or towards a visible loft, indicating simultaneous or oscillatory dual control between compass and pilotage mechanisms (Biro et al 2007; Armstrong et al 2013).

Olfactory Navigation and the “Olfactory Map”. Experimental deprivation of olfactory input, either by nerve section or anosmia, disrupts homing from unfamiliar locations in both naïve and experienced pigeons, establishing olfaction as necessary for development and expression of the map step (Wallraff 1988; Wallraff 2001; Gagliardo et al 2008; Gagliardo et al 2009; Bonadonna & Gagliardo 2021). Exposure to natural winds at the home loft during ontogeny is required for pigeons to associate wind-borne odor patterns with spatial position, forming an “olfactory map” that encodes regional gradients of atmospheric trace compounds (Bonadonna & Gagliardo 2021; Wallraff 2001; Wallraff 2005). Atmospheric analyses reveal stable large-scale gradients in ratios of volatile hydrocarbons over hundreds of kilometers, consistent with the precision of observed homing performance and supporting theoretical olfactory-gradient navigation models (Wallraff 2001; Wallraff 2005). Anosmic pigeons typically show random initial bearings and poor homing efficiency, even after extensive flight training, underscoring the centrality of olfactory information for true navigation beyond familiar terrain (Gagliardo et al 2008; Gagliardo et al 2009; Bonadonna & Gagliardo 2021; Wallraff 2001). The contributions of olfactory, visual, and solar cues vary systematically across spatial scales and familiarity contexts, and are summarized in Table 1 (Consensus 2026).

Table 1

Principal navigational cues across contexts: relative roles of olfactory, visual and solar cues

<i>Context / scale</i>	<i>Dominant map mechanism</i>	<i>Dominant compass mechanism</i>	<i>References in literature</i>
Unfamiliar, long-range	Olfactory gradients (“olfactory map”)	Sun compass; magnetic compass backup	Wallraff (1988); Wallraff (2001); Gagliardo et al (2008); Gagliardo et al (2009); Walcott (2005); Wiltschko & Wiltschko (2017)
Familiar regional area	Visual landscape + olfaction (redundant)	Sun compass modulating route choice	Wallraff (2001); Wallraff (2005); Gagliardo & Bingman (2024); Biro et al (2007); Armstrong et al (2013)
Final approach/ goal in sight	Visual pilotage; landmark-based hippocampal guidance	Sun compass still consulted	Gagliardo & Bingman (2024); Biro et al (2007); Armstrong et al (2013)

Solar Compass and Visual–Landmark Systems. Clock-shift experiments demonstrate that pigeons rely on a time-compensated sun compass both in unfamiliar and highly familiar environments: phase-advanced or -delayed internal clocks produce predictable angular deviations in initial bearings and even in short final approaches within sight of the loft (Walcott 2005; Armstrong et al 2013). Over familiar terrain, GPS-tracked birds may recapitulate stereotyped idiosyncratic routes based solely on learned landmarks when sun and learned compass direction are placed in conflict, yet route trajectories are often laterally shifted in the predicted compass direction, revealing an integration of landmark pilotage with solar compass orientation (Biro et al 2007). Within familiar areas, olfactory and visual information are functionally redundant: pigeons deprived of one modality can still home effectively by using the other, and visual guidance appears to depend on panoramic landscape structure rather than only on linear strings of discrete landmarks (Wallraff 2001; Wallraff 2005; Gagliardo & Bingman 2024). Neuroethological work links visual–landmark navigation to the hippocampal formation, which supports a map-like representation based on multiple independent landmark elements enabling direct pilotage over tens of kilometers (Gagliardo & Bingman 2024). Hippocampal lesions spare the ability to recall a sun-compass bearing learned at a site, but prevent formation of flexible, landmark-based spatial maps, yielding a residual “site-specific compass orientation” strategy rather than true pilotage. Electrophysiological studies reveal diverse spatially tuned cells in the pigeon hippocampal system—place-like, path and boundary cells—paralleling, but not identically matching, mammalian hippocampal organization and reinforcing its role in multi-scale spatial mapping (Hough 2022; Gagliardo & Bingman 2024). Sun-compass processing itself shows only limited lateralization. In outdoor beacon–sun conflict paradigms with monocular occlusion, pigeons using either eye can learn sun-compass guided spatial tasks, although subtle hemispheric asymmetries emerge in cue integration: left-eye/right-hemisphere birds may show different weighting of beacons versus solar azimuth and somewhat reduced learning speed (Griffiths et al 2020; Cioccarelli et al 2023). These findings suggest a bilateral but asymmetrically tuned visual–solar network embedded within the broader navigational circuitry.

Magnetoreception and Its Role within the Multimodal System. Conditioning experiments have demonstrated that pigeons can discriminate the presence versus absence of a local magnetic anomaly, with performance abolished by attaching a magnet to the cere, anesthetizing the upper beak, or sectioning the ophthalmic branch of the trigeminal nerve, while section of the olfactory nerve leaves discrimination intact (Mora et al 2004). These results support the existence of a magnetite-based receptor system in the upper beak, trigeminally mediated and capable of detecting magnetic irregularities (Mora et al 2004). Nevertheless, multiple field experiments show that section of the trigeminal ophthalmic branch does not impair homing from unfamiliar locations in either naïve or experienced pigeons, whereas olfactory nerve section consistently causes severe navigational failure (Gagliardo et al 2008; Gagliardo et al 2009; Bonadonna & Gagliardo 2021). Similarly, GPS-tracked birds subjected to a strong magnetic pulse, sufficient to re-magnetize ferrimagnetic particles irrespective of their anatomical location, exhibit unchanged initial orientation, route tortuosity, and homing efficiency, arguing against any essential role for ferrimagnetic receptors in the homing process at least under mid-latitude geomagnetic conditions (Holland et al 2013). Satellite telemetry in wild birds likewise provides robust support for olfactory but not magnetic-map based navigation: section of the olfactory nerve, but not of the trigeminal ophthalmic branch, disrupts large-scale compensatory movements during migration or incubation, while cage-based orientation experiments may still reveal trigeminally mediated magnetic effects under artificial conditions (Bonadonna & Gagliardo 2021). Collectively, these findings suggest that while pigeons possess a functional magnetic sense, likely trigeminally mediated and detectable in operant paradigms, its contribution to the map component of homing is limited or context-dependent. The geomagnetic field remains, however, a plausible auxiliary compass reference under overcast skies, in line with broader avian orientation literature (Walcott 2005; Wiltschko & Wiltschko 2017; Wallraff 1988; Holland et al 2013). Figure 1 shows the magnetoreception pathway and its role in guiding migratory behavior.

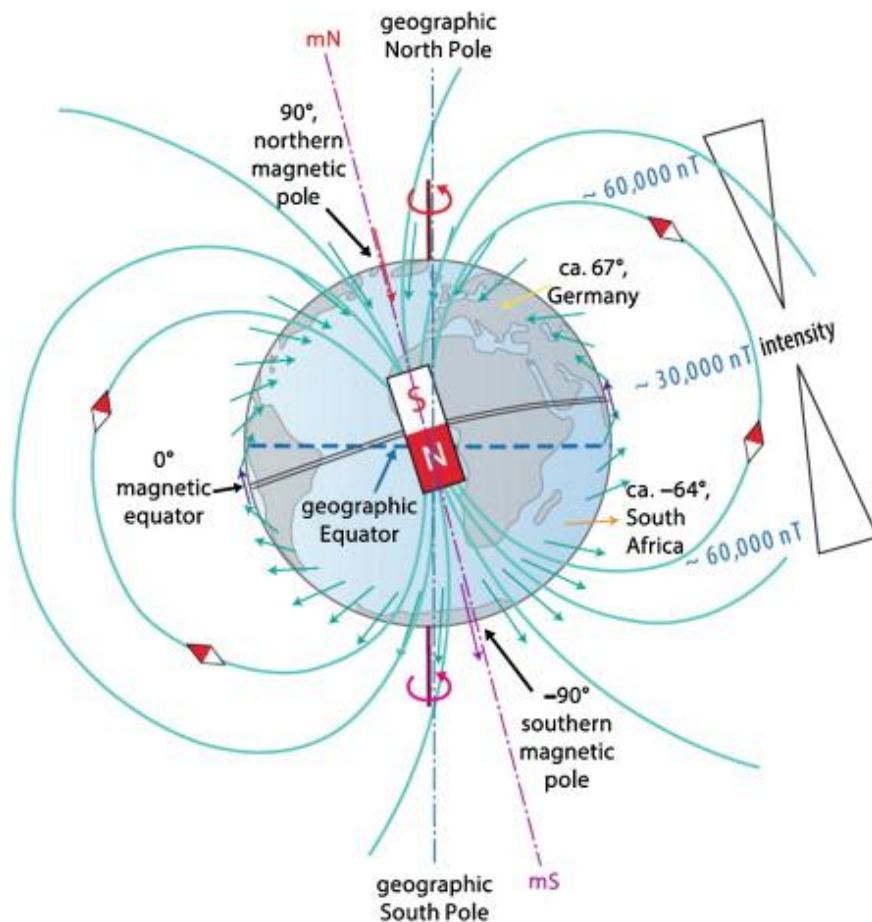


Figure 1. Magnetoreception in birds and its use for long-distance migration (Mouritsen 2015).

Conclusions. The navigation system of homing pigeons emerges as a highly sophisticated and flexible multimodal framework, rather than a hierarchy dominated by a single sensory modality. Strong empirical evidence supports the central role of olfaction in large-scale navigation, particularly in the formation and use of an “olfactory map” based on atmospheric gradients. This mechanism appears essential for true navigation from unfamiliar locations, as demonstrated by the profound impairment observed in anosmic individuals. Complementing the map component, the time-compensated sun compass provides a robust and consistently utilized directional reference. Its influence persists even in familiar environments and during the final approach phase, indicating that compass-based orientation is not abandoned when landmark information becomes available but instead operates concurrently. This dual-control mechanism reflects a dynamic integration in which compass cues can modulate or bias landmark-based routes.

Visual navigation, mediated largely by the hippocampal formation, becomes increasingly dominant at smaller spatial scales. Pigeons rely on learned landscape features and panoramic cues to establish stable, idiosyncratic routes, demonstrating a capacity for map-like spatial representation analogous, though not identical, to that observed in mammals. The redundancy between visual and olfactory cues in familiar areas further illustrates the system’s resilience, allowing compensation when one modality is compromised. In contrast, magnetoreception, while clearly present at a physiological and behavioral level, appears to play a secondary or context-dependent role in pigeon navigation. Experimental evidence suggests that trigeminally mediated magnetic input can support detection of magnetic anomalies and may contribute to compass orientation under specific conditions, such as reduced visibility. However, its contribution to the map component is minimal, as disruption of magnetic input does not significantly impair homing performance, unlike olfactory deprivation.

Overall, the integration of olfactory, solar, visual, and magnetic cues reflects an adaptive strategy that maximizes navigational accuracy across variable environmental conditions. Rather than relying on a fixed hierarchy, pigeons dynamically weight available information sources depending on familiarity, spatial scale, and sensory reliability. Future research should focus on the neural mechanisms underlying this dynamic weighting, the ecological constraints shaping cue use, and the reconciliation of laboratory-based findings with behavior observed under natural conditions. Such efforts will be essential for advancing a comprehensive understanding of animal navigation and its underlying biological principles.

Conflict of interest. The authors declare that there is no conflict of interest.

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