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Review

The avian olfactory system and hippocampus: Complementary roles in the olfactory and visual guidance of homing pigeon navigation

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Abstract

The homing pigeon is the foundational model species used to investigate the neural control of avian navigation. The olfactory system is critically involved in implementing the so-called olfactory map, used to locate position relative to home from unfamiliar locations. The hippocampal formation supports a complementary navigational system based on familiar visual landmarks. Insight into the neural control of pigeon navigation has been revolutionised by GPS-tracking technology, which has been crucial for both detailing the critical role of environmental odours for navigation over unfamiliar areas as well as offering unprecedented insight into the role of the hippocampal formation in visual landscape/landmark-based navigation, including a possible, unexpected role in visual–spatial perception.

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Introduction

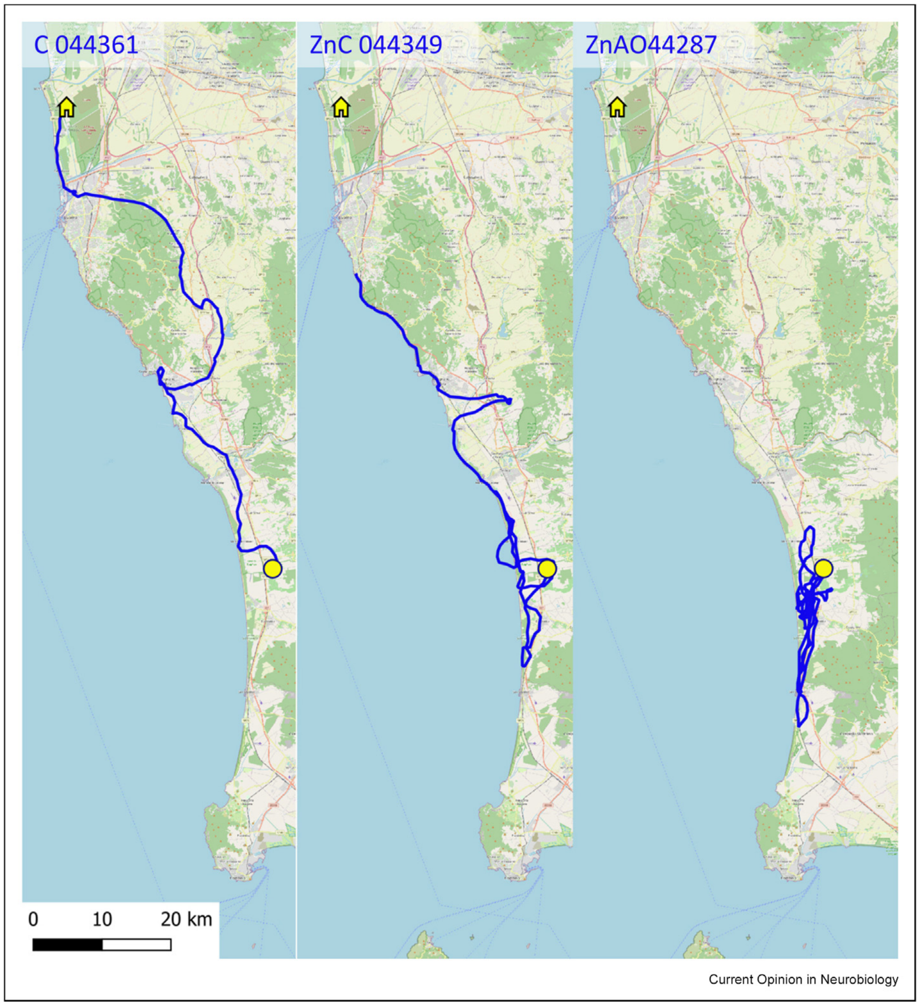
Birds are nature's supreme navigators and the behavioural, sensory, and neural mechanisms that are used to support their navigational ability have been most thoroughly studied in homing pigeons (*Columba livia*) [1–3]. The extraordinary ability of homing pigeons to find their loft even when displaced to distant, unfamiliar locations has always fascinated navigation researchers, and the theoretical conceptualisation of this ability, a positional or map sense combined with a directional or compass sense as developed by Kramer [4], still shapes conversations on bird navigation today.

Olfaction and the homing pigeon navigational map

While there is a general agreement on the existence of both sun and magnetic compasses in birds [5], understanding the sensory basis of the avian "navigational map" was for years a source of often hostile debate [6–9]. However, a large body of evidence collected over the last fifty years has supported the critical role of environmental odours as a source of spatial information used to support the homing pigeon "navigational map", i.e., a representation of space that enables pigeons to determine the direction home from unfamiliar, often distant locations [1,9,10]. Homing pigeons can learn an olfactory navigational map by associating wind-borne odours with their direction of origin [11,12]. Pigeons released at an unfamiliar location can then determine the direction home by identifying the odour profile at that location and recalling the direction of the wind that carried that odour profile to the home loft [1,9,13,14].

Given the demonstrated importance of atmospheric odours in shaping the navigational map, it is not surprising that pigeons possess the sensory/neural machinery for odour processing: they have a well-developed olfactory system [15]; odour stimulation induces electrical responses in the olfactory nerve [16,17] and olfactory bulb neurons [18,19]. The olfactory mucosa, olfactory nerves, and piriform cortex are involved in pigeon navigation from unfamiliar locations [1,9]. It is important to note that the effects of anosmia, an often-used experimental procedure to investigate olfactory navigation, is specific to a loss of navigational ability and not a consequence of some non-specific effect on behaviour, e.g., a loss of motivation or absence of sufficient brain activation, as suggested by some authors [20,21]. In fact, pigeons subjected to olfactory deprivation after being exposed specifically to the local environmental air at a release site successfully flew in the homeward direction, whereas pigeons exposed to purified air enriched with artificial, non-sense odours failed to orient homeward (Figure 1) [22,23].

Figure 1



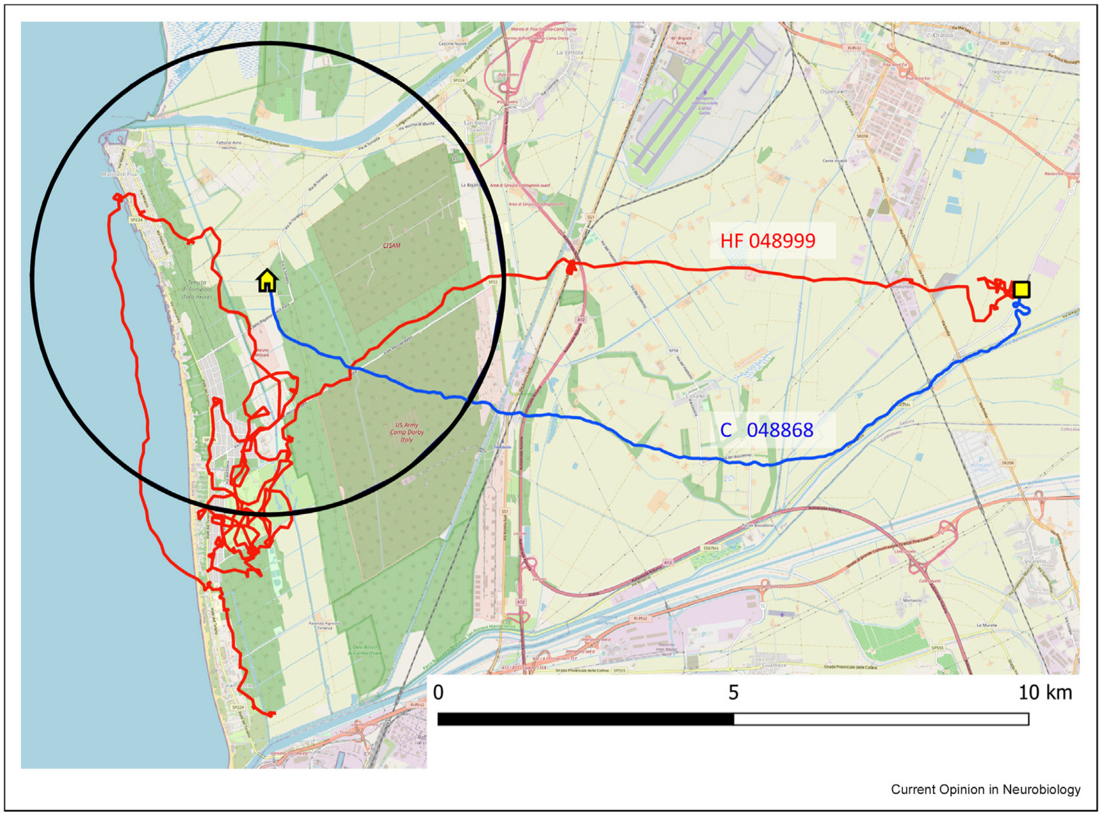
Representative tracks of pigeons released from a distant, unfamiliar release site subjected to different olfactory manipulations. The C pigeon was released without manipulation. The ZnC and ZnAO pigeons were exposed both during transportation to and at the release site to environmental air or artificial, nonsense odours diluted in purified air, respectively, prior to being made anosmic and released. Circle: release site location. House symbol: the home loft location. Data derived from Ref. [18].

The pigeon piriform cortex, homologous to the mammalian piriform cortex [24,25], is the telencephalic region that has been most studied in the context of olfactory navigation. Lesions to the piriform cortex result in a deficit in olfactory map learning [1] as well as the implementation of an already learnt olfactory map when pigeons are challenged with homing from unfamiliar locations [26]. Complementing the lesion effects on homing, the piriform cortex also displays upregulated neural activation, specifically an increase in Zenk-immediate early gene—labelled neurons, when pigeons are exposed to local odours at a distant, release-site location compared to odours from the home area near the loft [27]. Collectively, these observations identify the piriform cortex as a crucial node in the brain's olfactory map-processing network. Interestingly, Poo et al. [28] showed that the rat piriform cortex is composed of neurons coding for odour identity/recognition and neurons coding for allocentric space, elements that would need to be integrated during olfactory map learning.

Visually guided familiar landmark/ landscape navigation and the hippocampus

When navigating in areas where they have been before, particularly within the home area, homing pigeons can rely on a second map-like mechanism based on familiar, visual landmarks and landscape features [29,30]. At familiar locations, lesions at any level of the olfactory system do not disrupt homing [1,9] as familiar landscape features are a sufficient source of navigational information.

Figure 2



Representative tracks of an example intact (C, blue) and hippocampal-lesioned (HF, red) pigeon when released from a site about 15 km from home. The circle represents the 4-km buffer-radius around the home loft, where a landscape/landmark map is typically used to navigate to the home loft. Square: release-site location. House symbol: the home-loft location. Data derived from Ref. [35].

The existence of a map-like representation of familiar landmarks/landscapes immediately recalls the so-called "cognitive map" [31], and by implication, the hippocampus [32]. As the hippocampus of birds and mammals are homologous [33–35], it is not surprising that the avian hippocampus continues to be the principal target of research into the brain organisation of avian spatial-cognitive maps for both laboratory [36,37] and field research [33]. The early research on the relationship between hippocampus and pigeon navigation demonstrated that hippocampal lesions had no impact on their ability to fly off in the home direction from a distant, unfamiliar location, i.e., had no effect on the olfactory map, but it did result in pigeons being slower to return home or not returning at all [33]. This suggested an impairment occurring later during the homing flight, specifically when pigeons would transition from using their olfactory map to their familiar landmark/landscape map closer to home. However, it was not until the development of miniaturised GPS-tracking devices, which enable the reconstruction of a pigeon's entire flight home and are capable of remotely transmitting flight-path data from pigeons that do not return home, when the richness of hippocampal control of visually guided navigation was fully appreciated (Figure 2).

Flight path reconstructions have led researchers to conceptualise a pigeon's journey home as consisting of three phases. Soon after release, a pigeon typically, and more so from unfamiliar locations, displays a circling behaviour around the release site until taking off in a consistent, usually close-to-homeward direction (the so-called decision-making phase). A pigeon then continues its flight path homeward (the so-called en route phase) tending to follow its initial directional decision but periodically adjusting its flight direction based on newly encountered olfactory and/or familiar landscape information [9]. The last phase of a homing flight (the so-called local navigation phase) occurs when a pigeon arrives in the familiar area within a few kilometres of its loft, where the lower spatial resolution of the olfactory map would render it ineffective for navigation and the pigeon transitions to navigating by familiar, visual landscape/landmark features [38,39].

The GPS-tracking of hippocampal-lesioned pigeons confirmed their ability to orient homeward and approach the home area when released from a distant, unfamiliar location. More importantly, the same tracking highlighted the often tortuous or confused flight paths taken by the same pigeons as they transitioned to needing to navigate by visual landmark/landscape features near home [40], i.e., during the local navigation phase. Moreover, hippocampal-lesioned pigeons displayed a retrograde memory loss for the home area landscape features experienced before being lesioned [41]. Consistent with this observation, a ZENK-immediate-early-gene study revealed upregulated neuronal activity in the hippocampus when pigeons were released in the vicinity of the loft, although a greater number of labelled hippocampal neurons were found in pigeons homing from a more distant, unfamiliar location [27]. This latter finding supports the intuitive idea that when pigeons fly over unfamiliar locations, the hippocampus is recruited in learning the spatial properties of encountered landmark/landscape features—spatial learning that could support navigation when a pigeon would find itself in the same location in the future [33]. Shimizu et al. [42] also observed upregulated hippocampal neuronal activation when pigeons homed from a familiar location. In summary, GPS-tracking has enabled the robust demonstration that the hippocampus is essential for both the formation and implementation of a visual, familiar landscape/landmark-based map. One consequence of learning a familiar landscape map is that it would support the development of a faithfulness to the same route as pigeons repeatedly return home from the same location [29,30]. It is not surprising then that hippocampal-lesioned pigeons repeatedly released from the same location are impaired in developing the typically observed route fidelity [43,44].

Among the different topographic features composing a complex landscape, linear landmarks such as roads, rivers, and the edges of wood lots and fields, are often used by homing pigeons as “leading lines” to orient their flights even if following such an environmental leading line does not lead directly to home [45,46]. Similar to intact homing pigeons, hippocampal-lesioned pigeons can also follow leading lines as they are sometimes observed to fly along landscape edges [43,44]. However, GPS tracking has revealed notable differences between intact and hippocampal-lesioned pigeons in how they respond and use landscape leading lines while homing. By contrast with intact birds, pigeons without a hippocampus fail to consistently follow the same linear features when reaching the home area following repeated releases from the same locations [44]. In other words, while intact pigeons routinely incorporate leading-line landscape features into their landscape map, hippocampal-lesioned pigeons are impaired in doing so, explaining in part their diminished capacity to develop route fidelity. Even when released from unfamiliar locations, hippocampal-lesioned pigeons can display little tendency to have their flight paths altered by the presence of landscape features such as roads and villages, environmental features that can attract or repel intact pigeons. At one release location, GPS tracking revealed that intact homing pigeons consistently followed a road, which deviated from the direction home, whereas hippocampal-lesioned pigeons typically ignored that road and flew off directly towards home [41]. The frequent unresponsiveness of hippocampal-lesioned homing pigeons to visual environmental features has led to the speculation that the hippocampus is essential not only for supporting spatial cognition but is similarly important in the visual—spatial perceptual construction of a landscape scene.

A “site-specific compass orientation” navigational strategy is not hippocampal-dependent

Clock-shift procedures have provided important insight into the function of the pigeon hippocampus in navigation. Phase-shift manipulations, which alter the relationship between an animal’s circadian rhythm and the environmental light—dark cycle, result in pigeons misinterpreting the directional position of the sun azimuth, leading to predictable errors in the sun-compass orientation [47]. In other words, clock-shifted pigeons released at unfamiliar locations, and necessarily using their olfactory map to fix their position relative to home, typically display a predictable deviation in their flight directions as they misinterpret the sun’s azimuth.

Things are more complicated at familiar locations as phase-shift results in conflicting navigational information: the alignment of familiar landmark/landscape information is no longer consistent with the direction home indicated by the sun compass [48]. As such, pigeons relying directly on the familiar landscape for orientation, a strategy often referred to as pilotage, would be able to quickly reject the false directional information from the sun. By contrast, clock-shifted pigeons adopting a so-called “site-specific-compass-orientation” navigational strategy [49] would rely on their sun compass to orient their flight, displaying a pronounced deviation from the home direction, and indeed, when released from a familiar location, phase-shifted, intact pigeons display the ability to correctively re-orient homeward, presumably relying on their learnt landscape map. By contrast, hippocampal-lesioned homing pigeons fly off in the previously associated but now erroneous direction as indicated by their altered sun compass [50]. The importance of the hippocampus in supporting corrective re-orientation was dramatically highlighted when phase-shifted pigeons were released from a familiar location near the Mediterranean coast [50]. While intact pigeons erroneously flying towards the coast were able to reorient homeward before reaching the sea, several hippocampal-lesioned pigeons crossed the boundary between land and water, flying out over the open sea, sometimes for several kms. The failure of some hippocampal-lesioned pigeons to respect the landscape boundary between land and sea offers further evidence for a role of the hippocampus in visual—spatial perception [40].

A commonality between the olfactory and landmark/landscape maps

In our review, we have treated the olfactory and landmark/landscape maps as independent sources of spatial information with presumably different brain network organisations. However, neuroanatomically, there are reciprocal connections between the piriform cortex and parahippocampal region of the hippocampus [24]. Some evidence has suggested that, although not necessary for the operation of the olfactory map, the hippocampus can be involved in olfactory map learning. Homing pigeons can learn an olfactory map even if they are never allowed to fly freely around the loft as long as they are exposed to wind-borne odours [51]. However, in this unusual situation of a "captive" learning environment, hippocampal lesions block the learning of an olfactory map [1]. A parallel result is that hippocampal lesions impair the ability of homing pigeons trained in an outdoor arena to use the sun compass to learn the direction of a food cup [52]. We are not certain what this collection of findings means for understanding the brain organisation of homing pigeon navigation, but they do suggest something about the importance of the hippocampus in learning to associate sun-compass-derived directions with environmental stimuli, e.g., wind-borne odours or a food cup, when unable to freely fly.

Future directions

Regarding the hippocampal/brain-network basis of avian navigation, all the informative GPS-based research relied on what some may consider crude surgical lesions, and until recently, one could barely imagine recording the spatial response properties of hippocampal neurons in free-flying pigeons or behavioural procedures that would allow one to sample the spatial response properties of the same hippocampal neuron as a pigeon repeatedly flies over the same location. Simplistically put, what might a "place cell" look like in the context of a bird navigating an open field in a spatial scale of tens of kms? Vyssotski et al. [53] already provided a proof of concept for the possibility of "natural electrophysiology" as they successfully recorded GPS-interfaced EEG (electroencephalogram) in free-flying pigeons approaching land after being released from the sea. Although operating at a spatial scale of the size of a room, Agarwal et al. [54] recently remotely recorded the spatial-response properties of hippocampal neurons as barn owls (*Tyto alba*) flew between perches. Acknowledging the substantial technical gap between flying a few metres in a room and tens of kms in nature, the barn owl work does offer a path for gaining insight into the spatial characteristic of hippocampal neurons in the natural, navigational context of homing pigeons tracked with GPS. Furthermore, the tendency of homing pigeons to fly close to the same route when repeatedly released from the same location [30,43,44] can be exploited to repeatedly sample from the same population of neurons as pigeons fly over the same familiar terrain, allowing one to assess the temporal stability of any response characteristics.

There is substantial interest in understanding the function of lifespan neurogenesis in the dentate gyrus of the mammalian hippocampus [55,56]. Therefore, also worthy of more investigation is the potential importance of life-span neurogenesis in the avian hippocampus, which may enable birds to continually update their representations of space as new areas are explored (worth noting here is that neurogenesis in the avian hippocampus does *not* occur in any equivalent of a dentate gyrus [57]). Encouraging in this context, a recent paper characterising neurogenesis in the brain of adult, free-flying homing pigeons [58] specifically found a considerable number of newborn neurons in the hippocampal formation. What might be the spatial—cognitive consequences of blocking this neurogenesis? Also, a comparison of the patterns of neurogenesis in the hippocampal formation, piriform cortex, and other candidate brain regions relevant for navigation in pigeons subjected to different learning experiences/conditions, e.g., the acquisition of route fidelity with repeated releases from familiar locations or olfactory map learning in confined compared to free flight conditions, could reveal much about the importance of integrating new-born neurons into existing neural networks in support of dynamic maps of space.

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Declaration of competing interest

None.

Data availability

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