The Neural Basis of Long-Distance Navigation in Birds

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Abstract

Migratory birds can navigate over tens of thousands of kilometers with an ac-
curacy unobtainable for human navigators. To do so, they use their brains. In
this review, we address how birds sense navigation- and orientation-relevant
cues and where in their brains each individual cue is processed. When little
is currently known, we make educated predictions as to which brain re-
gions could be involved. We ask where and how multisensory navigational
information is integrated and suggest that the hippocampus could interact
with structures that represent maps and compass information to compute
and constantly control navigational goals and directions. We also suggest
that the caudolateral nidopallium could be involved in weighing conflicting
pieces of information against each other, making decisions, and helping the
animal respond to unexpected situations. Considering the gaps in current
knowledge, some of our suggestions may be wrong. However, our main aim
is to stimulate further research in this fascinating field.

INTRODUCTION

Birds embark on impressive migratory journeys that can cover thousands of kilometers. To find their way, birds need to sense and integrate information from a large number of cues in their environment.

Most long-distance navigation tasks consist of at least three different phases. The first phase involves long-distance orientation (the typical range in birds is more than ~200 km from the final goal), which must be based on global cues (such as celestial and/or geomagnetic information). Compass orientation is often important during this phase, which brings the birds into the homing range of their final goal (1). The second phase is a narrowing-in phase (the typical range in birds is ~1–200 km from the final goal), in which migratory birds are faced with a task similar to that of homing pigeons in release experiments. During this stage, a variety of learned local gradient maps probably relying on information from all available senses and cues are important (1). The third phase involves pinpointing the exact goal (the typical range in birds is less than ~1 km from the final goal), most likely on the basis of local landmarks such as specific trees that the birds could use to locate their nest sites (1). Very different cues are likely to be used during the three phases, and it is naïve to believe that a single sense or cue is used exclusively throughout. Birds integrating all available information from all potentially relevant orientation cues will have an evolutionary advantage over birds using only a single source of information.

Consequently, when a bird migrates, it has to integrate and weigh orientation-relevant information from all senses in its brain because it can fly in only one direction at any given point in time. In the present review, we first present, cue by cue, how birds can sense navigation- and orientation-relevant cues and where in the brain they are processed. Because, in many cases, little is certain, we combine neuroanatomical and behavioral information available from various birds and other vertebrates to make educated predictions as to which parts of a bird's brain could be involved. The aim is to stimulate future research in this fascinating field.

LONG-DISTANCE ORIENTATION IN YOUNG BIRDS DURING THEIR FIRST AUTUMN MIGRATORY JOURNEY: CLOCK-AND-COMPASS ORIENTATION

Young birds on their first autumn migration use a simple clock-and-compass strategy (also termed the calendar-and-compass strategy or the vector navigation strategy) to locate their wintering grounds (2–7). Their navigational systems do not involve any map-based feedback but instead work as follows: The birds fly in direction A for X days and then fly in direction B for Y days (although they can deviate from this strategy in some emergency situations, for instance, when they find themselves over water at dawn; see References 6 and 8). The clock-and-compass strategy requires only an inherited migratory direction, a circannual clock, and at least one compass.

Night-migratory songbirds are born with an inherited migratory direction (3, 9) and an annual time schedule (10). Night-migratory songbirds also possess or develop at least three different compasses prior to their first migratory journey: a sun compass (11, 12), a star compass (13, 14), and a magnetic compass (15–17). Young birds can find their migratory direction as long as information from at least one of these compasses is present (7, 18). Thus, young migrants have all the prerequisites required for performing calendar-and-compass orientation, but which parts of the brain are used to process the relevant information?

Circadian and Circannual Clock Information

Birds have endogenous circadian and circannual clocks (10). The circadian clock is directly involved in the sun compass, which requires time-of-day compensation (11, 12). The circannual clock is

essential for timing of migration and ensures that the birds know when to fly north and when to fly south (10). The existence of a circannual clock in migratory songbirds was shown in a classical experiment in which a group of garden warblers (*Sylvia borin*) was kept in a constant-daily-light regime at constant temperature and was given the same food throughout the year (10). Even with no access to external timekeepers, the birds retained their annual cycle periodicity. They showed migratory restlessness (Zugunruhe) only in spring and autumn, they grew their gonads in early spring, and they moulted and fattened up at the appropriate times (10).

The physiological basis of the circannual clock is not well understood. Several aspects of seasonality, such as migratory restlessness, are closely associated with season-specific changes in melatonin secretion (19). Melatonin also plays a key role in the circadian clock, and circadian rhythms and circannual cycles are likely to be closely linked (20).

The circadian clock in birds is much better understood than the circannual clock mostly because one cycle takes 1 day instead of 365 days and is thus much easier to study. The circadian clock is based on an ~24-h cyclic transcriptional feedback loop involving several proteins, including CRY1, CRY2, PER2, PER3, CLOCK, and BMAL1 (20, 21). In the wild, this transcriptional loop is entrained by the natural light-dark cycle through photoreceptor molecules in the retina, the pineal gland, and perhaps other brain regions (20–22).

The central clock of birds is most likely located in one or two hypothalamic brain nuclei: the medial suprachiasmatic nucleus (mSCN) and/or the visual suprachiasmatic nucleus (vSCN) (23, 24). These nuclei are anatomically and physiologically similar to the mammalian suprachiasmatic nucleus (SCN), and lesions of mSCN and/or vSCN resulted in disrupted circadian rhythms in several bird species (25–27). Similar to the mammalian SCN, the bird SCN is active during subjective day and excretes norepinephrine, which inhibits biosynthesis of melatonin in the pineal gland (20, 21). In both mammals and birds, melatonin secretion from the pineal gland into the bloodstream at night inhibits SCN activity (20, 21), and melatonin and norepinephrine also affect peripheral clocks elsewhere in the organism (20).

In mammals, circadian activity in the ventral subcompartment of the SCN synchronizes almost immediately to a time-shift, whereas the dorsal SCN shell lags behind (28, 29). If a similar phenomenon occurred in birds, it could, in theory, help birds determine east-west position after displacement on the basis of jetlag effects. However, migratory reed warblers, which compensated for a real 1,000-km eastward displacement (30), did not compensate for an identical simulated time-shift (31). Thus, jetlag effects are unlikely to be the main cue used by these birds to compensate for east-west displacements. To sum up, circadian and possibly circannual input into the birds' navigation system is probably based mainly on hormonal changes rather than on anatomical connections.

Celestial Compass Information

Many birds can use two celestial compasses: a sun compass and a star compass. However, to be functional, these compasses require learning during the premigratory period. Night-migratory songbirds are born with the information to look for rotating light dots in the sky and to interpret the center of rotation as north (13, 14, 32). Subsequently, they learn the geometry of the stars relative to the center of rotation so that, during migration, they no longer need to observe the rotation to detect stellar north (13, 14, 32, 33). To establish a sun compass, young birds must observe the path of the sun and must link the sun's positions to their circadian clock (12, 34).

Traditionally, the sun azimuth compass and the star compass are considered to be different. However, in both of these compasses, the axis of celestial rotation seems to be crucial, and hand-raised birds seem to be able to calibrate their magnetic compass by observing either the daytime

sky on which the sun and the polarized light patterns rotate (35, 36) or the nighttime sky on which the stars rotate (13, 37). Therefore, the sun and star compasses may be parts of a single celestial compass system in birds (38).

Celestial cues are detected by the birds' eyes and are processed in visual brain pathways. For the sun compass, observation of celestial movement must be integrated with circadian information. To directly perceive celestial movement, birds must detect velocities of 0.0042°/s. Some visual neurons in pigeons are indeed able to process very slow movements, but their lower sensitivity threshold is approximately 0.25°/s (39). These neurons were found in the nucleus of the basal optic root, a key structure of the accessory optic system that, together with the pretectum, contains neurons that respond specifically to the movement of large areas of the total visual field. The accessory optic system analyzes self-motion, not object motion (40). Neurons in the tectofugal visual pathway of pigeons participate in the analysis of object motion, but they prefer much higher velocities of 10–90°/s (40). Thus, there is presently no evidence that birds can process the extremely low velocities of celestial motion. Indeed, Alert et al. (38) tested pigeons with slowly rotating dot patterns and suggested that they were unable to detect the rotational center at velocities of less than 5.6°/s. Therefore, birds are unlikely to directly see celestial movement. But how then do they perceive stellar rotation?

A snapshot strategy could also detect the center of celestial rotation (38). The celestial compass could work by comparing the current star pattern with a memorized snapshot of the pattern from some prior time relative to fixed local landmarks. There is indeed strong evidence for the ability of pigeons to form snapshot memories; they can store stable panoramic views and subsequently use these memories for spatial orientation (41).

Yang et al. (42) reported that some neurons in the dorsal lateral geniculate nucleus (GLd) of pigeons are activated by low luminances of ≤ 1 lx. These cells could contribute to the perception of the starry night sky. Budzynski & Bingman (43) suggested that, in pigeons, left-sided Wulst lesions interfere with discrimination of distant landmarks. Kahn & Bingman (44) suggested that the pigeon hippocampus integrates visual features of the surroundings with spatial information to then construct navigational goals. Furthermore, lesions of the right hippocampus in pigeons interfere with learning the sun compass, but once this compass is learned, mainly the left hippocampus seems involved in using it (45).

If the celestial compass is based on a snapshot memory mechanism, we consider the following pathway most likely: Ascending visual pathways like the thalamofugal system and/or the tectofugal system plus their associative areas could represent and store the necessary visual information in a somewhat lateralized manner. In mammals, storage of visual patterns is often enabled in associative visual areas, and not in primary visual areas. If the same applied to birds, associative structures like the nidopallium frontolaterale (NFL), the nidopallium intermedium laterale (NIL), and the mesopallium ventrolaterale (MVL) could be crucial entities. It is possible that the asymmetry within the visual system is transposed onto hippocampal circuits without the hippocampus itself being lateralized (46). The hippocampal complex could also store and then retrieve this visual information for use in navigation (see **Figure 1**). The hippocampus and the area corticoidea dorsolateralis (CDL), which serves as an entry port to the hippocampus, have reciprocal connections to visual areas. Thus, memorized visual patterns within the visual system and within the hippocampal complex could be in constant exchange.

Magnetic Compass Information

The magnetic compass of migratory birds was discovered in European robins, *Erithacus rubecula* (15). It is an inclination compass (16, 47), which detects the angle between the magnetic field lines
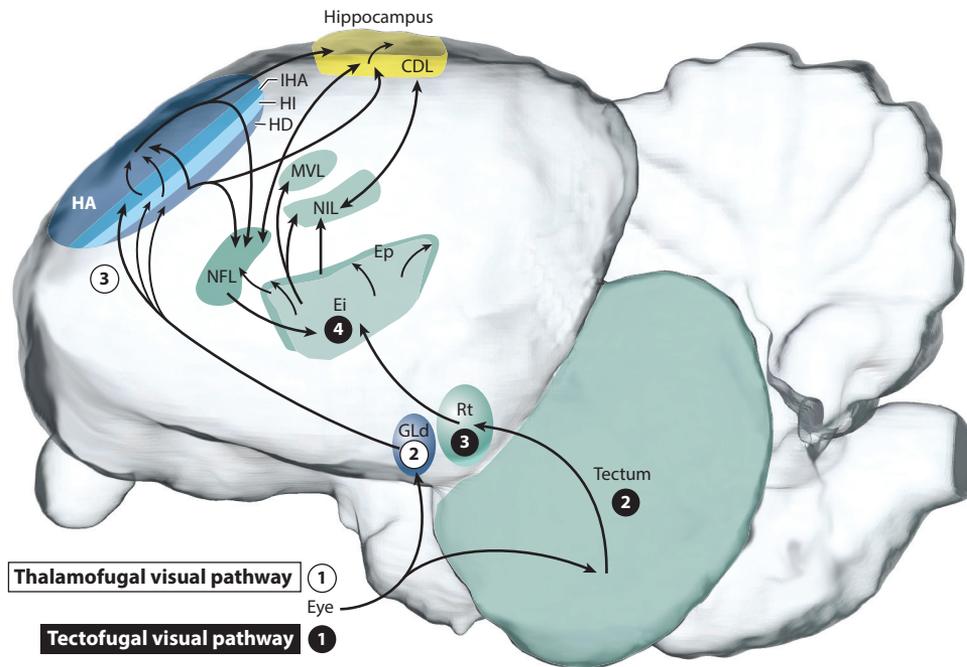
Figure 1

Schematic drawing of suggested celestial compass–processing pathways in the bird brain. The tectofugal visual pathway (eye > optic tectum > Rt > entopallium) and the thalamofugal visual pathway (eye > GLd > visual Wulst) are shown. Shown neuronal connectivities are summarized in References 143, 150, and 151. Abbreviations: CDL, area corticoidea dorsolateralis; Ei, entopallium internum; Ep, entopallial belt; GLd, dorsal lateral geniculate nucleus; HA, hyperpallium apicale; HD, hyperpallium densocellulare; HI, hyperpallium intercalatum; IHA, interstitial nucleus of HA; MVL, mesopallium ventrolaterale; NFL, nidopallium frontolaterale; NIL, nidopallium intermedium laterale; Rt, nucleus rotundus.

and the Earth's surface or gravity, but not the polarity of the magnetic field lines. Consequently, birds do not distinguish between north and south but rather distinguish between poleward and equatorward (47). The ability to sense magnetic fields is inherited, but at least in some birds, their magnetic compass needs to be calibrated from celestial cues to become functional (13, 35, 37, 48).

How do birds sense the Earth's magnetic field, and where in the brain is magnetic compass information processed? From a behavioral perspective, at least some birds seem to use stereotypic head scans to sense the Earth's magnetic field (49). From a biophysical perspective, sensing magnetic fields as weak as that of the Earth by using biologically available materials is not easy (50). At the present time, only two magnetosensory principles are thought to be physically viable in terrestrial animals (51): iron mineral–based magnetoreception and radical pair–based magnetoreception.

Compass needle–like structures based on the iron mineral magnetite are found in magnetotactic bacteria (52). These structures are often referred to as magnetosomes (52). Similar structures have repeatedly been suggested as the basis for avian magnetoreception (53) but have not convincingly been located within bird tissues. Other iron mineral–based structures located in the upper beaks of birds were long thought to be putative magnetic field sensors (54, 55), but these structures were recently shown to almost certainly be nonsensory (56–58). Thus, at present, no potentially magnetosensory iron mineral structures associated with nerve tissue and found at a consistent

location within many individuals of the same species have been discovered. Even though these two central requirements have not been satisfied, we cannot eliminate the possibility that iron mineral–based magnetoreceptive structures exist in birds.

In contrast, the second hypothesis—namely that the magnetic compass is based on a light-dependent, radical pair–based, chemical compass mechanism (50, 59–63)—has gathered significant experimental support. The primary sensory molecules are most likely a cryptochrome protein (60, 64–68), but which parts of a bird's brain process magnetic compass information?

If the avian magnetic compass is light dependent, the primary sensors should be in the pineal gland or in the eyes. Because birds with removed pineal glands can still use their magnetic compass (69), the primary sensors are almost certainly located in the retina. Retinal neurons in both eyes contain at least four different cryptochromes [CRY1a, CRY1b, CRY2, and CRY4 (67)]. Further-more, retinal ganglion cells in both eyes (64) and a forebrain area named Cluster N are by far the most active parts of the brain when night-migratory songbirds use magnetic compass information for orientation behavior (70–72). Cluster N is inactivated when the eyes are covered (70, 71, 73), and neuronal tracing showed that Cluster N is a small part of the visual Wulst, which receives its input from the eyes via the thalamofugal visual pathway [eyes → GLd → Cluster N (74)]. When Cluster N is surgically inactivated, night-migratory songbirds cannot use their magnetic compass, whereas their sun and star compasses remain functional (72). Because Cluster N is part of the thalamofugal visual pathway, this finding is strong evidence that the magnetic compass is light dependent, that the primary sensors must be in the eyes, and that birds perceive magnetic compass information as a visual impression (62). In a day- and night-migratory songbird, Cluster N is active only at night, and it may therefore be specialized for magnetoreception under low-light conditions, when it would not compete with, e.g., color vision (75).

Despite early claims to the contrary (76), the tectofugal visual pathway is almost certainly not involved in magnetoreception (62, 77–79). Thus, the first stations in the pathway process-ing light-dependent magnetic compass information in night-migratory songbirds are known (see **Figure 2**).

In addition to magnetic information, an inclination compass needs input from gravity sensors, which suggests that input from the vestibular system is involved. Wu & Dickman (80) reported magnetic field–triggered neuronal activation in the vestibular brain stem complex of pigeons. This activation disappeared after ablation of the lagena nerve (80). Furthermore, electrophysiological recordings suggested that there are magnetic field direction–sensitive cells in the same brain regions in pigeons (81). However, if there are magnetic sensors in the lagena, they are unlikely to provide magnetic compass information in night-migratory songbirds, because in Zapka et al. (72), the Cluster N–lesioned birds that could not use their magnetic compass had intact lagenas and lagena nerves.

Even if magnetic compass information is not sensed in the lagena, vestibular information still needs to be integrated with magnetic information in the brain. Such integration could take place in the hippocampus, which probably receives directional magnetic field line information from Cluster N (see **Figure 5** below) (82) and gravity information from the posterior thalamic nuclei (83). The posterior thalamic nuclei receive input from the vestibular sensory hindbrain complex (84, 85), which contains tilt-sensitive neurons (86).

LONG-DISTANCE NAVIGATION IN EXPERIENCED BIRDS: MAP-BASED NAVIGATION

Breeding and wintering site fidelities are as high as the survival rates in many migratory bird species (6). Thus, experienced birds achieve a precision of a few meters over a distance of more
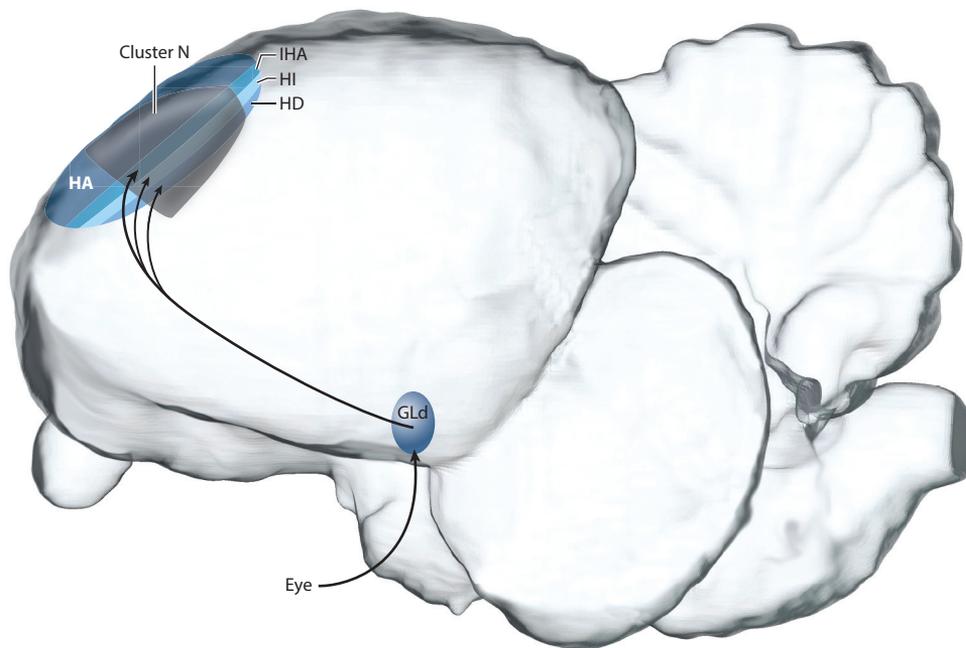
Figure 2

Schematic drawing of the suggested magnetic compass–processing pathway in the bird brain. Abbreviations: GLd, dorsal lateral geniculate nucleus; HA, hyperpallium apicale; HD, hyperpallium densocellulare; HI, hyperpallium intercalatum; IHA, interstitial nucleus of HA.

than 5,000 km. Such precision is not possible with a simple clock-and-compass strategy. Maps must have become part of the navigational system of experienced birds. The existence of experience-based maps has been demonstrated through displacement experiments: Whereas juvenile migrants are generally unable to correct for displacements (2, 4, 6, 7), experienced migrants can correct for displacements to unknown locations from their first spring onward (2, 30, 87, 88). Which cues are used in this map?

Map cues are highly multisensory and change during different stages of a long-distance navigation task (see Introduction, above). Map cues almost certainly include olfactory cues (89–91), landmarks (92), celestial cues (14), and geomagnetic cues (88, 93). We expect that most birds will use all these cues in concert. Which cues are most reliable will vary regionally, and thus their relative importance is also expected to vary (1).

Magnetic Map Information

The use of magnetically based maps has been reported in various bird species, but the existence, and the spatial accuracy, of maps is still heavily debated. Although some researchers studying pigeon homing consider homing pigeons using a magnetic map with a precision of a few kilometers to be a proven fact, others have boldly stated that the magnetic map in pigeons is nothing but "an evergreen phantom," i.e., nonexisting (47, 51, 94). If a detailed magnetic map exists, it remains a challenge to understand how a magnetic field–based map should be able to function on a scale of a few kilometers, because magnetic intensity and inclination vary only ∼3 nT/km and ∼0.009°/km in a background field of approximately 50,000 nT, in addition to which rather stochastic, daily

variability of 30–1,000 nT in random directions occurs (51). It is, however, easy to imagine that a magnetic map or signpost sense could function on a much larger spatial scale, and some songbirds seem to use magnetic cues at least as an approximate geographic signpost (88, 95). Very recently, a virtual magnetic displacement experiment finally unequivocally demonstrated that a long-distance migratory songbird can use a magnetic map for navigation (96).

It was long suggested that iron mineral–based structures in the upper beaks of birds might function as magnetic map information sensors (54, 55). These structures were claimed to be located in sensory nerve endings (dendrites) in the subepidermis at six specific spots along the lateral edges of the upper beak in a strictly bilateral symmetry. However, these findings (54, 55) were seriously challenged by a highly laborious study on >200 pigeons in which the previously described iron-containing structures were found to be macrophages rather than magnetosensitive neurons (56, 57). Mouritsen (58) independently confirmed that the structures described by Treiber et al. (56, 57) included the structures described by Falkenberg et al. (55). However, technical limitations of the Prussian blue staining method used mean that other iron mineral–based magnetic sensors could have remained undetected (58).

Despite the controversy on the sensor level, a growing body of evidence suggests an involvement of the ophthalmic branch of the trigeminal nerve (V1)—the only nonolfactory nerve entering the upper beak—in magnetoreception. Several studies using surgical ablation of V1 reported significant effects on birds' abilities to detect magnetic field changes (97) and found a significant decrease in magnetically induced neural responses in trigemino-recipient hindbrain structures after V1 ablation (77, 78). Thus, V1 does seem to carry magnetic information, even though the primary sensors remain unknown. In the present review, we consider only actual cutting of V1 as convincing evidence for the relevance of V1 in specific tasks (for our reasoning, see Reference 62).

The magnetic information carried by V1 is unlikely to provide compass information, because intact trigeminal nerves are neither necessary nor sufficient for magnetic compass orientation (72, 98). In contrast, V1 most likely carries positional magnetic information to the brain because migratory reed warblers can compensate for a 1,000-km displacement only if V1 remains intact (88) and because strong magnetic pulses thought to remagnetize any iron-containing sensors led to deflected orientation in adult but not juvenile migratory birds (7, 99).

In which parts of the brain is V1-associated magnetic information processed? V1 passes the trigeminal ganglion to terminate in the principal (PrV) and spinal sensory (SpV) nuclei of the trigeminal nerve (100). Magnetic field stimulations in European robins and pigeons strongly activated medial parts of the SpV as well as a crescent-shaped region ventral to the PrV (PrVv) (77, 78). This activation significantly dropped both when V1 was cut and when the ambient magnetic field was compensated (77, 78). Thus, the SpV and PrVv are very likely to be involved in magnetoreception.

The SpV receives topographically ordered afferents from all branches of the trigeminal nerve (100). In the mallard duck, the SpV shows bilateral intratrigeminal projections within the SpV and to the PrVv and prominent ipsilateral projections into various cerebellar lobes (101).

The only known projection of the PrV to higher brain centers is a direct connection to the nucleus basalis (NB), which is located in the rostrocaudal telencephalon, via the quintofrontal tract (102, 103). However, whether the PrVv also projects to the NB is unclear. Moreover, it is difficult to demonstrate whether the NB is involved in magnetoreception, because it does not express any known neuronal activity–dependent immediate early genes such as Egr-1 or c-fos and electrophysiological studies related to magnetoreception are tricky.

The NB projects, probably via multisynaptic connections through the NB shell, to the trigeminal part of the nidopallium frontale (NFT) (102, 103). The NFT shows ample projections terminating in various other forebrain regions, such as arcopallial substructures as well as the
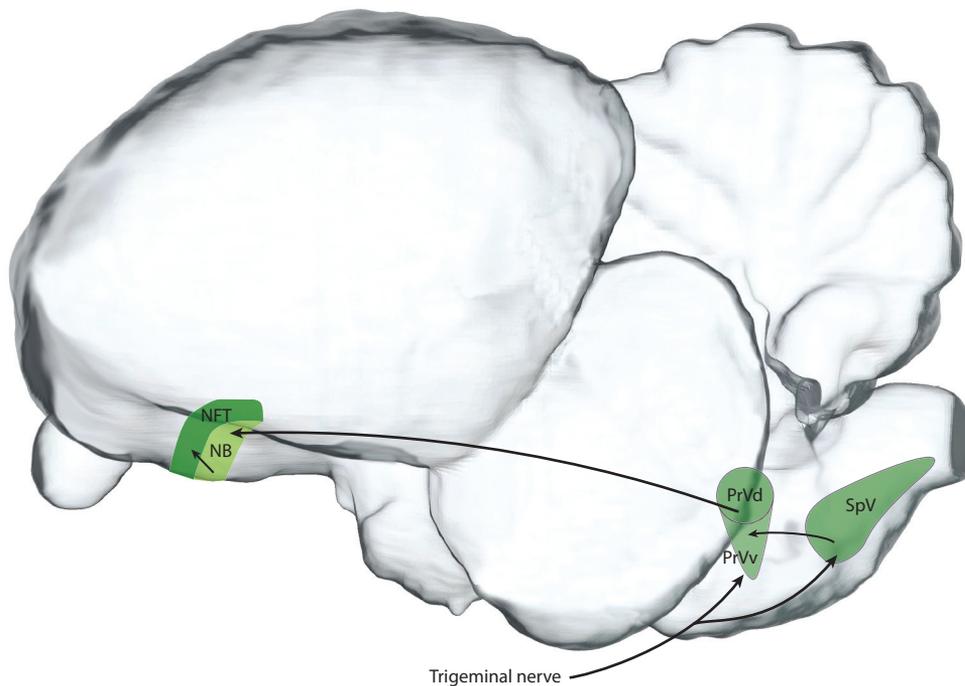
Figure 3

Schematic drawing of the suggested magnetic map information–processing pathway in the bird brain.
Abbreviations: NB, nucleus basalis; NFT, trigeminal part of the nidopallium frontale; PrVd, principal
sensory nucleus of the trigeminal nerve, dorsal part; PrVv, principal sensory nucleus of the trigeminal nerve,
ventral part; SpV, spinal sensory nucleus of the trigeminal nerve.

caudolateral nidopallium (NCL) (102, 104). Input from the lagena may also be involved in sensing
magnetic map information (80, 81). We currently consider the pathway illustrated in **Figure 3** to
be the most likely brain circuit for the processing of magnetic map information.

Olfactory Map Information

The role of olfactory cues in navigational maps has been extensively studied in homing pigeons.
For instance, pigeons home toward a wrong direction when they cannot smell at the actual release
site but sense the olfactory information from a previous mock release area (105). Similarly, fans
blowing artificial odors from specific directions strongly affect the homing directions of pigeons
(106). Olfactory cues also play an important role in experienced pelagic birds, which breed on
small oceanic islands and have huge homing ranges over the open ocean. For instance, Cory's
shearwaters displaced by 800 km were disoriented when deprived of their sense of smell, but not
when magnetically disturbed (91). However, an odor-based map is most likely not a coordinate
map in pigeons but a gradient map providing information only about the direction of displacement
(107). Such a map may be based on detecting location-specific ratios of some key odors. Indeed,
Wallraff & Andreae (108) repeatedly collected samples of air from a large number of sites within
200 km of a pigeon loft and discovered that the ratios, but not the absolute concentrations, of several
volatile organic compounds provide fairly stable spatial gradients in the atmosphere. Simulation

experiments suggested that these stable ratios and gradients provide sufficient information for successful homing (108).

The olfactory pathways in the bird brain are well known. Receptor cells in the olfactory epithelium in the nose cavities sense olfactory information. Their axons constitute the olfactory nerves, which terminate ipsilaterally in the olfactory bulbs (OBs). The OBs project bilaterally onto a wide array of structures that include the piriform cortex (CPi), the prepiriform cortex (CPP), the hyperpallium densocellulare (HD), parts of the amygdala, and components of perihippocampal structures. The CPi and CPP further interact with parts of the visual system, with the prefrontal NCL, and with additional limbic structures. Thus, the CPi and the associated CPP are dominated by olfactory fibers but also interact with hippocampal, limbic, executive, and visual areas (109, 110).

The relevance of smell for navigation is possibly reflected in the neuroanatomy of birds. OBs of homing pigeons seem to be enlarged compared with OBs of nonhoming pigeon breeds (111). OBs are also spectacularly enlarged in birds that use olfactory cues for navigation and foraging, such as seabirds (89). Manipulations of the olfactory system, such as plugging the nostrils (112), anaesthetizing the olfactory mucosa (113), transecting the olfactory nerve (90, 114), and ablating the CPi (115), generate remarkable and lateralized disruptions of initial orientation and homing performance in pigeons (107).

Patzke et al. (116) used immediate early genes to compare the brain activation patterns in three groups of pigeons: birds released at an unfamiliar site, birds transported and kept at the same site but not released, and birds released near their loft. The highest numbers of Erg1-positive neurons were found in the CPi of pigeons released at the unfamiliar location. Many Erg1-positive neurons were also found in the birds kept at the release site. Birds released in the vicinity of their loft showed no significant increase in CPi activation. These results implicate the CPi of pigeons in the processing of olfactory map cues and indicate that navigation is a multisensory process whereby familiar visual landmarks become more relevant than olfactory cues close to the goal.

In summary, we consider the following pathway to be most likely for processing of olfactory map cues in the bird brain: The OB projects heavily onto the CPP and CPi. Both structures interact with the hippocampal complex and transfer olfactory map information via these pathways so that this information can be used for spatial orientation (117). Smaller projections also exist between the OB and the visual HD. In addition, the HD also interacts with the CPP and CPi, thereby possibly integrating visual landmark information and olfactory map information (see **Figure 4**).

Landmark Information

When pigeons learn to home toward their loft, their flight paths become less variable over time, suggesting that they learn a maplike structure of the environment and use this structure for piloting (92, 118). Individual pigeons may take different routes but often employ prominent visual landmarks as orientation or turning points (92, 119, 120). This map of memorized places may be associated with compass instructions but may also be sufficient in guiding the journey, at least for some time. This last option may depend on the reliability of the memory storage of landmarks.

But how do birds use landmarks? Do birds orient by prominent objects, or are they able to use the overall geometry of the surrounding landscape, which is accessible from a number of sites within a given area? Studies in different avian species indicate that both kinds of cues are employed but, depending on task conditions, to different extents (121, 122). Data from several avian species suggest that the left hemisphere predominantly processes single landmarks, whereas the right hemisphere predominantly processes geometric information (121–123).

Landmarks are visual objects used for navigation. They are therefore processed within the visual system, stored in visual association areas, and then used by the hippocampal complex for
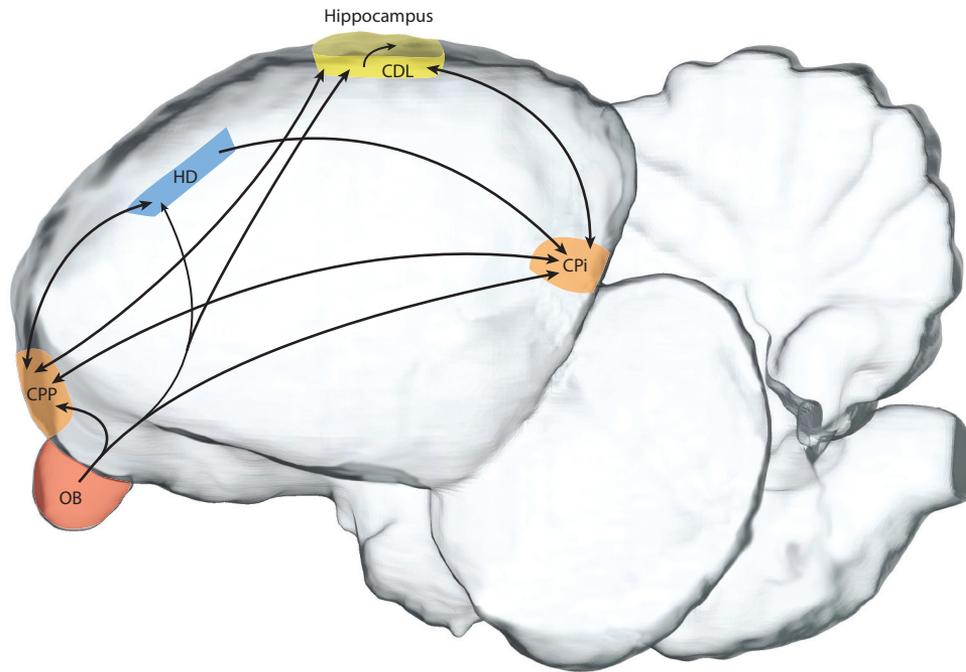
Figure 4

Schematic drawing of the suggested olfactory map information–processing pathway in the bird brain.
Abbreviations: CDL, corticoidea dorsolateralis; CPi, piriform cortex; CPP, prepiriform cortex;
HD, hyperpallium densocellulare; OB, olfactory bulb.

navigational computation. In essence, the relevant pathways may be identical to the ones discussed above in the context of celestial compass processing (see **Figure 1**), but very little is known at present.

Integration of Map Cues: The Role of the Hippocampus in Navigation

In every vertebrate class studied, the hippocampus has been found to play a critical role in spatial memory and cognition, and birds have provided the most compelling evidence (124). Food-caching birds can memorize hundreds of caches over many months (125), hippocampal volume in food-storing bird species is higher than in related nonstoring species (125), and migratory subspecies of white-crowned sparrows have more hippocampal neurons and larger hippocampi than do nonmigratory populations (126).

The current evidence suggests that the bird hippocampus primarily supports learning and utilization of maplike, spatial representations of familiar landmarks that can be used to guide navigation over familiar space (127). Indeed, in pigeons, hippocampal lesions do not seem to affect orientation from unfamiliar locations but primarily affect navigation around the home area when previously learned landmarks are available (117). Memorized landmarks should also be relevant for migrants in familiar areas and during the narrowing-in and pinpointing phases of long-distance migration (see Introduction, above).

It is important to stress that birds can navigate for some time without an intact hippocampus (128). However, hippocampal circuits become relevant when novel input necessitates corrective

maneuvers, as shown in an elegant experiment in which GPS-tracked pigeons that were both anosmic and clock shifted were released over familiar territory (117). Due to the clock shift, birds usually started out in the wrong direction but later corrected their flight paths. Whereas control animals quickly reoriented toward the loft, hippocampus-lesioned birds took longer to correct and often neglected prominent landmarks such as the coastline (117).

Birds orient in space by using not only a single landmark but also the relative location of several landmarks (geometry coding). Left and right hippocampi in pigeons seem to contribute differently to single-landmark navigation and geometry-based navigation (129, 130). It is possible, however, that this lateralization is transposed onto the hippocampus only by the asymmetry of the visual system, in which the left hemisphere encodes primarily for single features, whereas the right hemisphere excels in the analysis of feature relations (131). In addition, left, but not right, hippocampal lesions in pigeons resulted in impaired navigational map- and sun compass–based learning (45, 132).

Our understanding of the neurobiological substrates of very near space navigation (in lab-based arenas) in mammals has undergone a revolution since head direction cells (133, 134) and place cells (135) were found in the rat hippocampus and grid cells (136) were found in the entorhinal cortex of the rat brain. The head direction cells in perihippocampal structures are anatomically the starting point (134). Each of these neurons has a preferred angle of the animal's head direction relative to arena landmarks such that each neuron constitutes an individual compass of which the summed activity vector points toward the direction of the animals' heads. This compass information may be fed into medial enthorinal grid cells, which fire at repeating activity spots that are arranged on a hexagonal grid (136). The grid size seems to increase systematically from the dorsal to the ventral parts of the dorsocaudal medial region of the entorhinal cortex (136). Grid cells may serve functions that resemble an odometer or map. These findings raise some intriguing questions. Do head direction cells relating to global cues such as magnetic and celestial compass directions exist in any animal? Do grid cells scale up to kilometers or even thousands of kilometers when animals explore much larger spaces in the wild? Recent work on bats has shown that grid and head direction cells extend into three-dimensional spaces (137–139). Furthermore, grid cells can stretch and compress when the environment is deformed, possibly due to input from border cells in the subiculum (140). Is there evidence for the existence of these cell types in birds?

Presently, the answer is no. In the left hippocampi of pigeons, Siegel et al. (141) discovered some cells that may represent a track toward a goal. However, no such cells are known in mammals. The search for navigation-related neurons in the bird hippocampus is hampered by the difficulties in comparing the hippocampi of mammals and birds. Although there is no serious dispute as to the homology of the mammalian hippocampus and the avian hippocampus, putative homologies of hippocampal and parahippocampal subfields remain unclear. The mammalian enthorinal cortex likely corresponds to the avian dorsolateral hippocampus (142). Similarities and differences in other subareas of the avian and mammalian hippocampi are less clear, making comparisons difficult. This reality is especially true for the dentate gyrus, which may be a de novo structure that exists only in mammals (124).

In conclusion, the neuronal mechanisms underlying long-distance spatial memory and cognition in birds are mostly unknown. However, given the obvious conceptual similarities between place cells, grid cells, and head direction cells on the one hand and maps and compasses on the other hand, might the same underlying set of mechanisms exist in birds and smoothly scale between near and distant space?

Given the current knowledge, we suggest that magnetic compass information, celestial compass information, visual landmark and geometry information, olfactory map information, and magnetic map information have to reach the hippocampus. The path of the visual information to
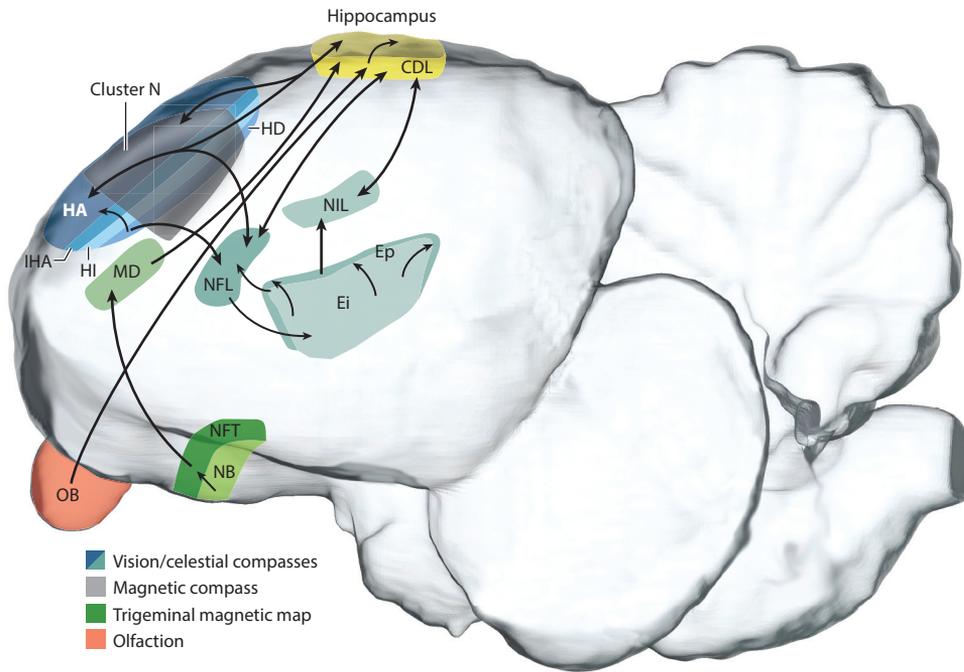
Figure 5

Pathways to the hippocampus that could store, integrate, and retrieve information about maps and compasses. The different sensory streams—vision/celestial compasses, magnetic compass, trigeminal magnetic map information, olfaction—are denoted by different colors. The shown neuronal connectivities are summarized in Reference 143. Abbreviations: CDL, corticoidea dorsolateralis; Ei, entopallium internum; Ep, entopallial belt; HA, hyperpallium apicale; HD, hyperpallium densocellulare; HI, hyperpallium intercalatum; IHA, interstitial nucleus of the HA; MD, mesopallium dorsale; NB, nucleus basalis; NFL, nidopallium frontolaterale; NFT, trigeminal part of the nidopallium frontale; NIL, nidopallium intermedium laterale; OB, olfactory bulb.

the hippocampus is outlined above in the discussion of snapshot memories of the stellate compass. We have no information on the projections from Cluster N that could transfer magnetic compass information to the hippocampus, but such information may take a parallel route to the visual output from the visual Wulst. If magnetic map information was processed in the trigeminal pathway, it could enter the hippocampus via the projections of the NFT to the mesopallium dorsale and then via the CDL to the hippocampus (82). Olfactory information directly reaches the CDL but could also be transmitted via the CPi (**Figure 5**).

WHERE DOES ALL THIS INFORMATION COME TOGETHER IN THE BIRD FOREBRAIN?

Birds need to integrate many sensory inputs carried by diverse ascending sensory brain pathways in their forebrain to properly navigate over long distances. Where in the forebrain does all this information come together?

One option is the NCL, which is a center of higher-order sensory integration. Sensory input from the trigeminal, visual, and olfactory streams reach the NCL via a set of interconnected pathways, which show considerable overlap in their respective termination fields (104). In addition,

the NCL receives afferents from various limbic structures that could inform it about ongoing motivational and emotional processes. Last but not least, the NCL is a convergence zone between ascending sensory and descending motor pathways and, as such, projects to all motor output areas (143). Could the NCL—in addition to its many other functions—be the navigational decision-making center in the bird brain where data from all navigation-relevant cues are weighed against each other and a decision is made to fly in a particular direction at any given moment in time?

Converging evidence from anatomical, electrophysiological, behavioral, and neurochemical studies suggests that the NCL is a functional analog to the mammalian prefrontal cortex and is thus firmly associated with the generation of executive functions (144). Executive functions are a cluster of cognitive processes that describe the ability of an organism to spontaneously generate efficient strategies when relying on self-directed, task-specific planning. Consequently, the NCL participates in functions in which sensory input is categorized and connected to learned output patterns, information is temporarily held for later action, response strategies are changed according to new information, responses are selected relative to contextual cues, and goals are chosen on the basis of their subjective value (145). Thus, the NCL may play a key role in navigation as a higher cognitive structure that sets goals, selects appropriate actions, and alters intermediate strategies when new and unexpected information becomes available.

Although all relevant sensory information seems to come together in the NCL (see **Figure 6**), this does not mean that the master map and compass can be found there. As outlined above, the NCL is involved in setting goals and in weighing evidence when conflicting stimuli are to be integrated for a decision. The map as a position device may be represented in a distributed manner in diverse sensory areas. The hippocampus has access to these multiple maps to compute navigational directions on the basis of the absolute and relative locations of stimuli that provide positional information. When flying over known territory, birds have to integrate compass information with the many maps. Again, it is unlikely that there is a compass area in the bird brain. It is more likely that compass information resides in the sensory streams but that both the hippocampus and the NCL interact with these sensory areas to perform two diverse tasks. First, the hippocampus could interact with structures that represent maps and compass information to compute and constantly control navigational goals and directions. Second, the NCL could be involved in weighing conflicting evidence, in coming to a decision, and in helping the animal respond to unexpected situations. When birds flying over unknown territory are relying only on compass information, the NCL could integrate all bodily information on motivation, timing, hunger, and fatigue to organize the moment-to-moment decisions of a journey.

THE ORGANIZATION OF MOTOR OUTPUT

Once a bird's brain has decided which way the bird should fly, it must send this signal to the motor output systems. Like mammals, birds have two different descending systems for motor control. The first consists of fibers from the pallial areas that descend to the brain stem and the spinal cord. The second is the diverse subpallial system, in which the somatomotor basal ganglia pathways are especially relevant for motor actions. We outline both systems here (see **Figure 7**).

The first system is the tractus occipitomesencephalicus (TOM), which originates in the arcopallium intermedium (AI) and descends through the thalamus and the dorsolateral tegmentum (146). The TOM likely plays a key role in all aspects of motor control that involve manipulations with the beak (103). The other system is the tractus septomesencephalicus (TSM), which originates in the hyperpallium apicale (HA) and descends with various terminations along its path through the ventral brain stem to the cervical spinal cord, where it synapses predominantly in the medial part of the dorsal horn of the upper seven cervical segments (147). The TSM thus
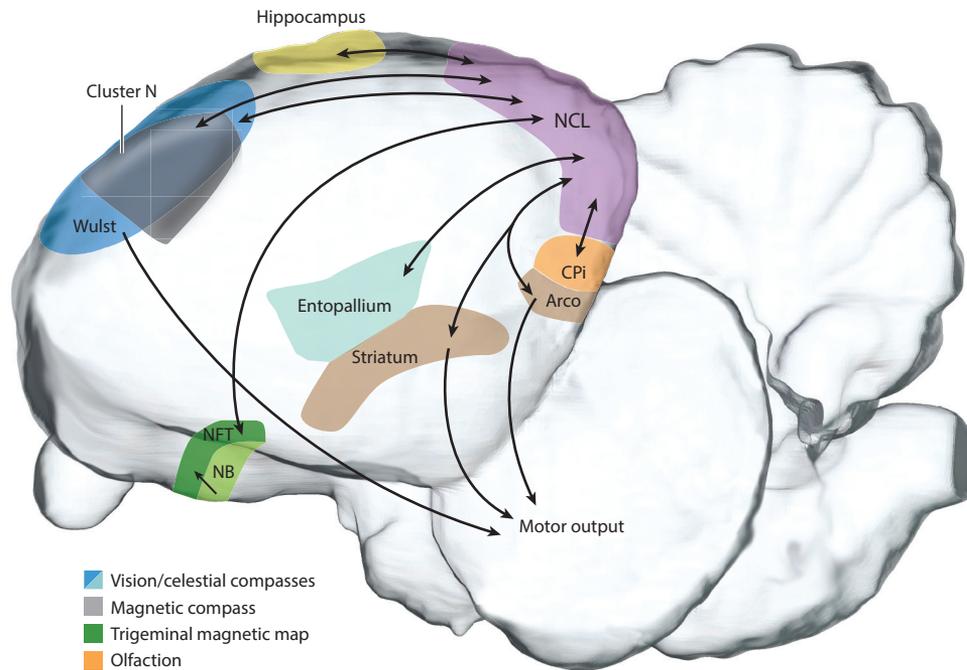
Figure 6

Schematic drawing of the navigation-relevant brain regions, all of which are connected to the NCL in the bird brain. Sensory streams are color coded. The NCL interacts with the hippocampus and has direct access to motor output pathways. The shown neuronal connectivities are summarized in Reference 143. Abbreviations: Arco, arcopallium; CPi, piriform cortex; NB, nucleus basalis; NCL, caudolateral nidopallium; NFT, trigeminal part of the nidopallium frontale.

resembles the mammalian pyramidal tract and may be especially relevant for flight-related motor control (148).

Using behavioral molecular mapping, Feenders et al. (149) described a cluster of pallial areas that are active during limb and body movements like flight and wing whirring. The activated nidopallial and mesopallial areas may be motor clusters that are connected directly or via at most one intermediate structure to the AI, the HA, and the NCL (see **Figure 7**). Thus, these areas are linked to structures that control descending motor pathways (the AI and HA) or that modify behavioral plans on the basis of new information (the NCL).

OUTLOOK

The anatomical connections within the avian brain and which sensory systems provide the inputs to which brain areas are generally well understood (143). In comparison, our understanding of the functional links between anatomy, specific sensory information, and orientation/navigation decisions mostly trails behind.

To understand the specific circuits and cognitive processes responsible for the processing of navigational information in birds, multidisciplinary approaches are needed. These approaches should combine (*a*) focal neuronal tracing; (*b*) cleverly designed behavioral paradigms; (*c*) navigation-induced immediate early gene expression and/or electrophysiological studies; and
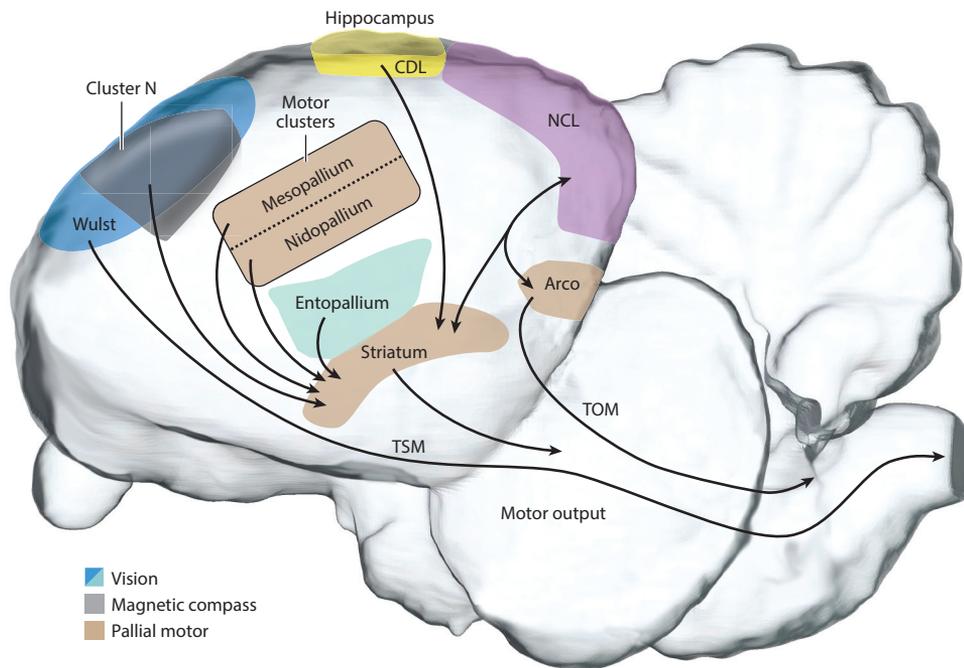
Figure 7

Schematic drawing of the motor output pathways of the bird brain. Neuronal streams are color coded according to their origin. Shown neuronal connectivities are summarized in Reference 143. Abbreviations: Arco, arcopallium; CDL, corticoidea dorsolateralis; NCL, caudolateral nidopallium; TOM, tractus occipitomesencephalicus; TSM, tractus septomesencephalicus.

(*d*) loss-of-function approaches targeting specific circuits and investigating the effects on behavior, gene expression, and/or electrophysiology.

Furthermore, we urgently need bold experiments that attempt to bridge near space (lab arenas and short-distance homing) and far space (flights covering hundreds or even thousands of kilometers). For instance, do head direction cells, place cells, and grid cells exist in birds; can they be related to global cues; and do they scale to kilometers or even thousands of kilometers?

DISCLOSURE STATEMENT

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72. Demonstrates that magnetic compass information is processed in Cluster N; thus, birds "see" magnetic fields.

77. Demonstrates that the trigeminal nerve is also involved in magnetoreception that is probably map related (see Reference 88).

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