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How do migrating birds find their way?

迁徙鸟类如何发现其迁移路线?

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摘要 迁徙鸟类的导航是一个相当复杂的过程, 涉及鸟类对环境的感受、神经生理反应、自由基对的化学反应等多种机制. 鸟类之所以能准确地找到其迁徙路线, 外界信号感受与神经处理机制的共同作用至关重要. 外界信号感受是迁徙鸟类对信号因子(偏振光、气味、次声波、地磁场等)的识别过程. 可能存在的信号感受有视觉感受、嗅觉感受、听觉感受、地磁感受. 神经机制是迁徙鸟类感受到外界信号后, 传递信息到大脑特定区域, 进行整合分析, 对迁徙方向做出准确判断的过程. 已发现的神经机制有视觉神经机制、嗅觉神经机制、磁感受神经机制. 尽管在外界信号感受与神经机制方面还有许多未解决的难题, 新技术与模式动物的应用将有助于进一步揭示确切的机制.

关键词 迁徙鸟类, 导航, 嗅觉, 听觉导航, 地磁导航, 神经机制

迁徙鸟类导航是一个复杂而有趣的生物学问题, 也是一项引人注目的研究内容. 早在1873年Darwin[1]就曾提到动物导航, 他推测动物可能运用航位推测法进行长距离迁徙. 遗憾的是, 当时并没有人深入探究鸟类导航的机制问题. 鸟类导航过程由信号感受机制与神经机制共同完成. 信号感受机制在于识别外界信号因子, 而神经机制在于将信号进行整合处理, 形成导航地图, 完成准确的迁徙定向. 迁徙鸟类导航机制的研究发展迅速, 学界已经提出了许多模型与假说. 本文结合近10年该领域研究的新进展, 总结、归纳了迁徙鸟类导航的几种主要假说与机制, 提出了迁徙鸟类导航研究中依然存在的主要科学问题, 并重点回顾了迁徙鸟类的导航机制问题和未来的发展趋势.

1 迁徙鸟类的信号感受机制

鸟类具有多种灵敏的方向感受机制, 根据对不同环境信号因子的识别, 可以将其感受信号机制分为4大类、9小类(表1)[2~10].

1.1 视觉感受——天文导航

鸟类能利用太阳方位角、星辰、偏振光等天文现象确定迁徙方向[11]. 一天内的不同时间, 太阳方位角以每小时π/12的速率变化, 不同太阳方位角, 飞行轨迹不同, 但是最终的方向能保持一致[12]. 许多夜间迁徙鸟类在晴朗夜空中也能利用星辰进行定向导航. 靛蓝彩鹀(*Passerina cyanea*)在星辰由北向南改变后其定向也会发生相应变化, 证实鸟类在晴朗夜空能利用星辰位置完成导航[13]. 而在阴天, 偏振光则成为鸟类导航的依据. 旋转偏振光*e*矢量轴, 鸟类会改变其头部方向[2].

1.2 听觉感受——次声波导航

某些鸟类的听觉十分灵敏, 能感受到低频次声波(0.05 Hz). 山脉、地壳等产生的次声波(0.1~10 Hz)比高频声波的衰减更弱, 能传播到很远的区域, 理论

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表 1　9 种导航假说[2~10]

Table 1　Nine kinds of navigational hypotheses[2–10]

Ⅰ假说	Ⅱ假说	年份	提出者
天文导航 (视觉)	太阳导航	1950	Kramer[5]
	星辰导航	1957	Wagner和Sauer[8]
	偏振光导航	1982	Able[2]
嗅觉导航	镶嵌图假说	1971	Papi等人[6]
	梯度图假说	1974	Wallraff[9]
	嗅觉激活假说	2009	Jorge等人[4]
听觉导航	次声波导航	1977	Yodlowski等人[10]
地磁导航 (第六感)	磁铁石假说	1978	Gould等人[3]
	化学磁感受	1978	Schulten等人[7]

上会形成利于定位的声波梯度[14]. Hagstrum等人[15~17]通过大气传播模型发现家鸽(*Columba livia domestica*)能利用巢位特异性次声波地图，实现定向，而且北大西洋暴风雨活动引起的次声波季节变化会影响北半球鸽子的归巢情况. 切除家鸽耳蜗破坏听壶放飞后，只有少数听力受损个体能准确返航，进一步证明家鸽归巢定向可能通过感受次声波强弱实现.

1.3　嗅觉感受——嗅觉导航

由于鸟类感受气味的嗅球很小，一直以来，鸟类学家都认为鸟类的嗅觉能力很低，是退化的功能器官. 然而，Steiger等人[18]对鸟类嗅觉受体基因的研究表明，许多鸟类都具有极其敏锐的嗅觉. 鸟类能通过识别空气中的气味和气味的浓度进行导航[19]. 研究者先后提出了3种嗅觉导航的假说：镶嵌图假说(mosaic map hypothesis)、嗅觉激活假说(olfactory activation hypothesis)和梯度图假说(gradient map hypothesis).

镶嵌图假说认为，鸟类可以通过识别风向中的气味与巢位的关系，达到准确导航(图1(a))[6,20]. 嗅觉激活假说认为，嗅觉受体通过激活某种导航机制在定向中发挥作用(图1(b))[4,21]. 但是对该假说进行的野外实验不支持激活导航机制，激活假说只是为嗅觉干扰家鸽导航提供了一个可选择的解释[22]. 梯度图假说则认为，较大地理尺度上空气中可能存在气味浓度梯度，不同气味的浓度差异与地理距离形成坐标系，被鸟类用于导航定向. 一旦特异性气味化合物形成的梯度被识别，鸟类就能通过释放地点气味浓度确定所处的位置(图1(c, d))[9,20,23,24].

1.4　地磁感受——地磁导航

目前已有确切证据证明，鸟类能感知地球磁场的强弱和方向，确定其在地球上的大概位置，并能形成磁场地图，指引其迁徙导航. 行为学和生理实验支持鸟类存在两种磁导航假说：磁铁石假说与化学感受假说[25].

(ⅰ) 磁铁石假说.　蜜蜂腹部和家鸽头部相继发现磁物质的富集，证明其可能与导航有关[3,26]. 对灰胸绣眼鸟(*Zosterops lateralis*)的强磁脉冲和神经生理研究，发现对其上喙施加强磁脉冲，其头部转向施加脉冲的方向[27,28]. 虽然在鸟类的不同部位都发现有磁性颗粒存在，但是这些颗粒的磁感受器功能尚待进一步研究.

(ⅱ) 化学感受假说.　1978年，物理学家提出感光分子反应的自由基对(radical pair)模型来解释鸟类感知磁场的机制[7]. 欧亚鸲(*Erithacus rubecula*)行为学实验发现，鸟类地磁导航依赖于某些特定波长的光[29]. 随后Ritz等人[30]提出光感受器模型，进一步完善了自由基对化学反应的假说与机制. 目前对隐花色素感受器、化学感受机制与弱磁场放大机制上已有普遍的共识.

隐花色素感受器. 隐花色素(cryptochrome, CRY)具有由3个色氨酸组成的色氨酸三联子(tryptophan triad, TRP), 其氨基端光裂解酶区域(photolyase-related region, PHR)能非共价结合辅因子FAD (flavin adenine dinucleotide). 鸟类在日光下30 min后，绿光能激活CRY1a, 支持隐花色素CRY参与化学感受反应、感知地磁场强度和方向的观点[31,32].

化学感受机制. 光子激发鸟类视网膜上隐花色素的色氨酸三联子，产生一个电子并传递给氧化态的FAD, 形成了与自旋方向相反的单重激发态自由基对或与自旋方向平行的三重激发态自由基对. 单态和三态的分子能转化到长时间存在的FAD^-, 并引起视网膜视紫红质构象变化，产生电信号传递到Cluster N区(图2)[25,33].

化学放大机制. 地磁场强度变化范围为30~60 μT, 在鸟类体温下自由基对几乎不可能感应地磁强度(50 μT)[34]. 研究发现，鸟类中存在将弱地磁强度放大的机制，该机制取决于FAD-TRP与FAD-维生素C光循环以及FAD-TRP内自由基对的反应速率(图3)[35]. k_D和k_F为自由基$F^{\cdot -}$和$D^{\cdot +}$回复到激发态时的反应速率,

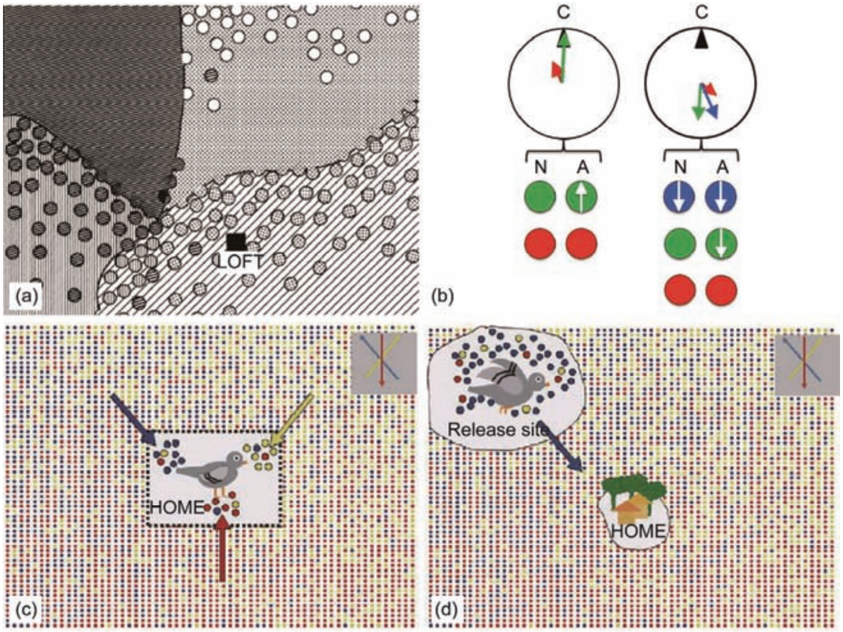

图 1　嗅觉导航 3 种假说[4,20,21,23]. (a) 镶嵌图假说：不同气味形成的镶嵌图；(b) 嗅觉激活假说：参与实验的不同组均值向量，N为导航假说，A为激活假说．左侧路径整合信息，绿色代表飞行途中的合成空气和人工气味，红色代表只有合成空气无人工气味．右侧地图信息，蓝色表示错误释放点的一组能嗅到自然空气，绿色表示能嗅到人工气味，红色为对照．箭头表示方向，无箭头的表示随机分布；(c, d) 梯度图假说：不同颜色的小圆点代表不同的气味化合物分布梯度，箭头表示方向．(c) 学习期：归巢鸟类会学习风中的气味和风向的关系．(d) 操作期：释放点的鸽子会收集当地气味信息

Figure 1　Three hypotheses about olfactory navigation[4,20,21,23]. (a) Mosaic map hypothesis, formed by various odors; (b) olfactory activation hypothesis, mean vectors of experimental groups, N, presenting navigation hypothesis, and A, showing activation hypothesis. The left is process of integrating information, green circles, showing synthetic and artificial odors on flight way, red circles, presenting artificial odors. The right is map information, blue and green circles presenting that birds can smell natural air and artificial odors, respectively, and the red is control treatment. Arrows stand for distributing directions; (c, d) gradient map hypothesis, dots presenting odorous gradient, and arrows showing directions. (c) Learning phase, birds learning to distinguish the relation between odors and wind direction. (d) Operational phase, pigeon detecting local odors

$k_D/k_F>1$，磁场被增加；$k_D/k_F<1$，磁场被减弱．当k_D和k_F在10^{-1}~10^3 s^{-1}的范围，放大系数能达到5~20[35,36]．

2　导航定向的神经机制

鸟类对不同信号的感知，最终需在大脑不同神经区进行整合分析，形成准确的导航图．目前的神经生理学研究，已发现了控制视觉导航、嗅觉导航和地磁导航的神经处理区域与相关机制．

2.1　视觉神经机制

鸟类的海马结构(hippocampe，HF)对其空间认知具有重要作用，也被认为是参与太阳导航的重要脑区(图4(a))[37,38]．海马结构损伤实验表明，HF受损的鸟类不能准确使用太阳导航定位[39]．大脑左右半球在鸟类导航中有不同程度的参与度．鸟类左右大脑半球在处理空间和矢量信息时是平行过程，而右半球对几何信息处理有一定的优势[40]．

2.2　嗅觉神经机制

梨状皮层(piriform cortex，CPi)是鸟类接收嗅球信息的主要区域，能分析处理气味信息(图4(b))[38,41]．鸟类左右侧梨状皮层在处理气味信息时具有不对称性．全球定位系统(global position system，GPS)定位实验也发现右鼻孔堵塞的鸽子运动轨迹更弯曲，左侧鼻孔嗅到气味后表现更多的探索性活动，而右侧嗅觉系统更多涉及对导航图的操作[22,42]．嗅觉系统分析表明，CPi支配的嗅球细胞数目在同侧和对侧区域是对称排布，进一步验证了左右CPi的嗅觉处理功能[43]．

2.3　磁感受神经机制

行为学研究表明，鸟类能感受地磁场，从而进行地磁导航．目前认为三叉神经是磁铁石感受机制的神经区域，而Cluster N区是化学感受机制的神经区域．

(ⅰ) 三叉神经脑干复合体．尽管磁铁石感受水平还存在争议，但是已有大量实验证据表明，三叉神

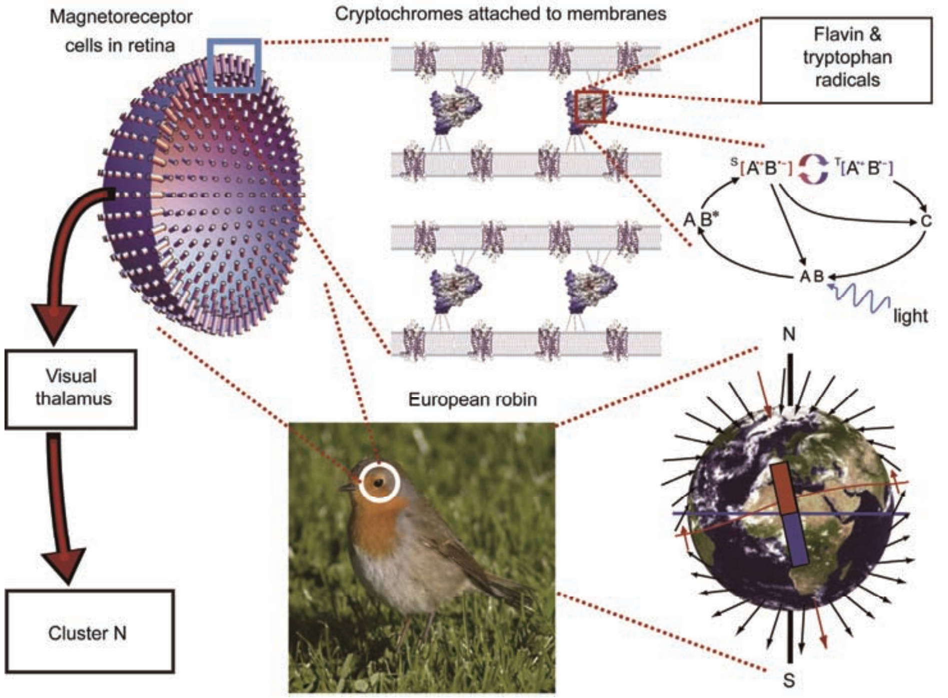

图 2　(网络版彩色)化学感受机制[25,33]. 视网膜上的隐花色素吸收光子, 形成FAD-Try自由基对, 其相对于地磁场矢量的方向决定了反应的量. 如果CRY与光受体外侧磁盘膜相连, 就会产生有序的结构, 视网膜不同部位会产生不同反应量相互对照, 提供可视的指南

Figure 2　(Color online) Chemosensor mechanism[25,33]. The cryptochromes (CRYs) absorb photons, forming FAD-Try radical pairs in the retina, whose direction relating to geomagnetic field vector decides the reaction yields. An ordered structure was produced, if the CRYs connected with the outer membrane disks of the photoreceptors, and various reaction yields respond to different parts of the retina could provide a visual compass

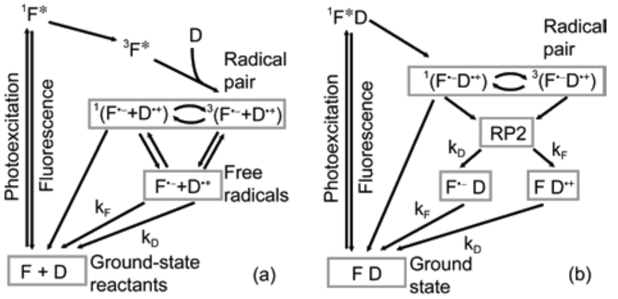

图 3　化学放大机制示意图[35]. (a) FAD分子间自由基对反应; (b) CRY分子内的自由基对反应. 在持续低强度光激发下, 只有自由基和基态反应物有较高的浓度. 其余种类使用期仅有微秒时长, 并且明显表现低光化学反应水平. 当强磁场启动, 自由基回复到基态变得低效, 光循环再次平衡到更多自由基对, 相应较少基态分子状态, 结果 $^1F^*$荧光减少. 反应过程中k_D和k_F的值决定了感受到的磁场是否被放大

Figure 3　Schematic mechanism of chemical amplification[35]. (a) Free radicals reaction among FADs; (b) free radicals reaction within CRYs. Free radical and ground state substrates kept high concentration under sustained low intensity light stimulating. Other species just kept a few microseconds and obviously represented low level of photochemical reaction. When stimulated by high-intensity magnetic field, free radicals became inefficiency to produce ground state substrates and kept higher concentration, then resulting to reduce $^1F^*$. Detected magnetic field was determined to be amplified by k_D and k_F

经(trigeminal nerve, V1)眼分支参与磁感受. 切断V1的鸟类感应磁场变化的能力丧失, 而且后脑的V1接收器的磁诱导神经反应显著降低(图4(c))[38,44,45]. ZENK蛋白标记神经元活性实验发现, 当欧亚鸲处于每3 h维持30 s磁场变化时, 三叉神经脑干复合体附近的三叉神经主要区域(PrV)和脊髓束(SpV)的神经元有磁活性, 表明PrV和SpV能传递磁信息到更高级的大脑区[40].

(ⅱ) 神经簇N区(Cluster N).　视网膜神经节细胞和前脑Cluster N区是夜间迁徙鸟类地磁导航过程中最活跃的部分(图4(d))[38]. Cluster N是离丘脑视觉通路的一部分, 在昼夜迁徙鸟类中, Cluster N只在晚上激活, 证明了磁导航的光依赖假说[46~48]. 鸟类中Cluster N区左右大脑半球在处理磁信息中也具有不对称性. 欧亚鸲右脑一侧Cluster N神经元活动有显著的优势, 迁徙鸟类可能具有在迁徙和日常生活中神经活动间的转换能力[49].

3　迁徙鸟类准确导航的实现过程

鸟类长距离迁徙活动, 通过视觉感受和地磁感

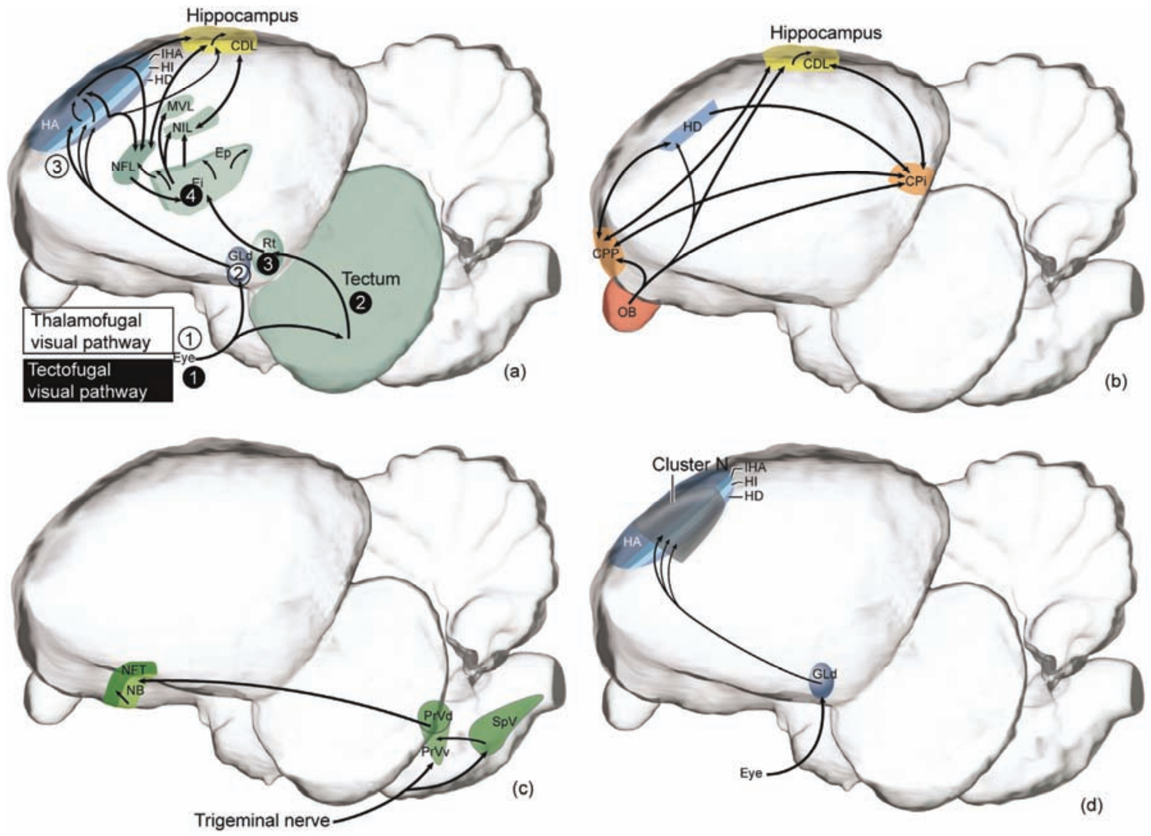

图 4 (网络版彩色)导航的神经回路[38]. (a) 天文指南的脑区及通路; 离顶盖视觉通路(眼睛>视顶盖>圆核(nucleus rotundus, Rt)>内大脑皮层)和离丘脑视觉通路(眼睛>背侧膝状核(dorsal lateral geniculate nucleus, GLd)>视觉突); (b) 嗅觉信息处理途径; (c) 磁颗粒神经通路; (d) 化学感受神经通路. CDL: area corticoidea dorsolateralis, 皮质背外侧区域; CPi: piriform cortex, 梨状皮质; Ei: entopallium internum, 皮质内核; CPP: prepiriform cortex, 前梨状皮质; OB: olfactory bulb, 嗅球; Ep: entopallial belt, 内大脑皮层带; GLd: dorsal lateral geniculate nucleus, 外侧膝状体背核; HA: hyperpallium apicale, 上皮质头部; HD: hyperpallium d ensocellulare, 上皮质背部; HI: hyperpallium intercalatum, 上皮质黑质; IHA: interstitial nucleus of HA, 上皮质头部间位核; MVL: mesopallium ventrolaterale, 旧大脑皮层腹外侧; NB: nucleus basalis, 基底核; NFL: nidopallium frontolaterale, 新脑皮层额外侧; NFT: trigeminal part of the nidopallium frontale, 新脑皮额部三叉神经; NIL: nidopallium intermedium laterale, 新脑皮层中外侧; PrVd, PrVv: principal sensory nucleus of the trigeminal nerve, 三叉神经主要区域; SpV: spinal sensory nucleus of the trigeminal nerve, 脊髓束

Figure 4 (Color online) Neural circuits of navigation[38]. (a) Celestial compass-processing pathways and brain areas, the tectofugal visual pathway (eye>optic tectum>Rt>entopallium) and the thalamofugal visual pathway (eye>GLd>visualWulst); (b) olfactory compass-processing pathways and brain areas; (c) magnetic particle-processing pathways and brain areas; (d) light-dependent magnetic compass-processing pathways and brain areas. Abbreviations: CDL, area corticoidea dorsolateralis; CPi, piriform cortex; Ei, entopallium internum; CPP, prepiriform cortex; OB, olfactory bulb; Ep, entopallial belt; GLd, dorsal lateral geniculate nucleus; HA, hyperpallium apicale; HD, hyperpallium d ensocellulare; HI, hyperpallium intercalatum; IHA, interstitial nucleus of HA; MVL, mesopallium ventrolaterale; NB, nucleus basalis; NFL, nidopallium frontolaterale; NFT, trigeminal part of the nidopallium frontale; NIL, nidopallium intermedium laterale; PrVd, PrVv, principal sensory nucleus of the trigeminal nerve; SpV, spinal sensory nucleus of the trigeminal nerve

受完成定向，而嗅觉与听觉导航在校正迁徙方向上发挥作用[50]. 在迁徙过程中，大脑必须权衡从各个感官收集来的信息，以保证在一定时间朝着一个方向迁徙[38].

3.1 信号感受器共同作用扫描地理信息

大量行为学实验表明，迁徙鸟类能通过对不同线索的综合利用，以达到准确导航的目的(图5)[51]. 长距离迁徙鸟类往往最先利用地磁场进行导航，然而地磁场并不能一直提供准确的定向. 例如，在日出和日落时，美洲草鹀(*Passerculus sandwichensis*)会使用靠近地平线的偏振光校正地磁导航，获得完整的定向系统[50].

3.2 神经处理器相互协作控制导航过程

鸟类需要整合许多前脑不同神经路径的感受信

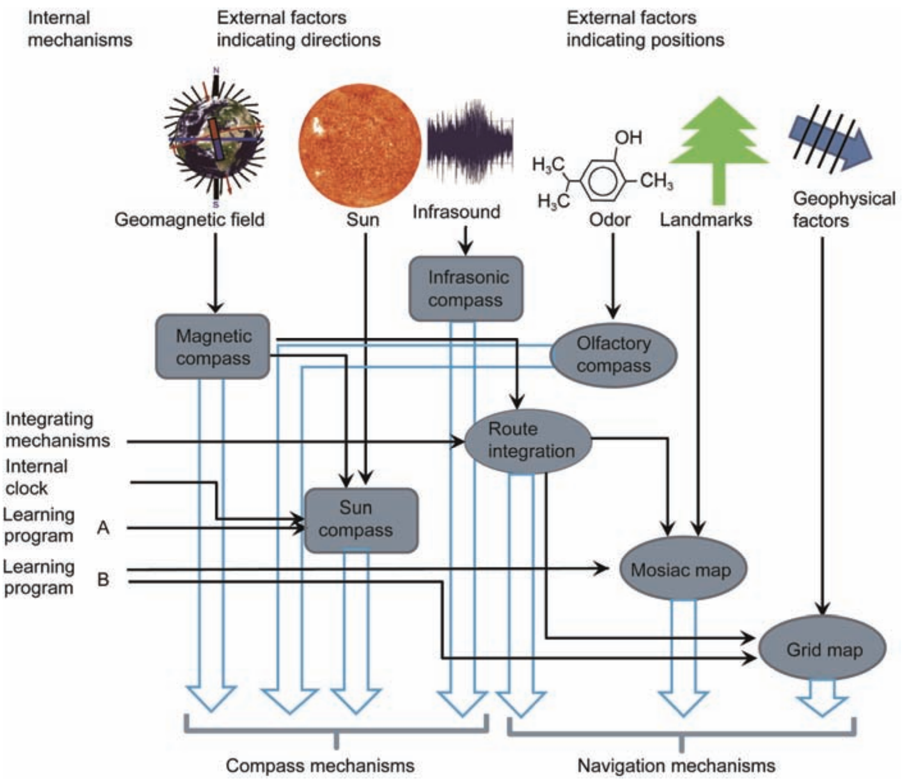

图 5 (网络版彩色)鸟类通过先天与学习整合利用不同导航系统[51]

Figure 5 (Color online) Birds integrate different navigational systems through inherent and acquired abilities[51]

息，并生成合适的导航图用于长距离迁徙，这是多个神经区域相互协作的过程．该过程包括导航地图的绘制、导航目标的判断以及动力输出的控制．

海马结构(HF)在整合导航地图中主要发挥了地图学习、使用和空间路标再现的作用(图6(a))[38,52]．因此，HF可能和呈现地图和指南信息与控制导航目标、方向的某些结构互作实现导航图的绘制．前脑的巢皮质尾侧(caudolateral nidopallium, NCL)是高级感觉整合中枢，感觉信号经内部连接通路从三叉神经、视觉、嗅觉到达NCL (图6(b))[38,53]. NCL可能作为目标设置的高级认知结构，参与输入信息的分类与输出学习的模式，并通过改变新信息反应策略和对前后线索的应答进行导航目标选择[54]．一旦导航图谱和导航目标确定，就需要向动力输出系统发出信号，鸟类可以通过大脑皮层-脑干/脊髓纤维束系统与多亚大脑皮层系统两个下调系统控制动力的输出(图6(c))[38,55~57].

4 迁徙鸟类导航研究中存在的问题

目前鸟类迁徙导航的机制都是基于大量的行为学证据，在具体导航线索感受机制、神经认知和学习等机制上仍然存在许多问题．考虑到目前学科与实验技术的发展，简洁地归纳了迁徙鸟类导航研究方法上的问题以及亟待解决的研究难点．

4.1 方法与模式

比较神经解剖学研究常只关注同种个体不同条件下的神经组织特征，如果考虑不同物种迁徙行为、学习记忆行为之间的联系，可能会发现迁徙鸟类特有的活性脑区．对于传统实验技术(普鲁士蓝染色法等)的局限性，可以利用全基因组筛查、Crisp/Cas9等先进的技术进行弥补．蝗虫(*Schistocerca gregaria*)利用偏振光的神经机制，以及斑马鱼(*Danio rerio*)、果蝇(*Drosophila melanogaster*)磁感受能力的发现，可以将斑马鱼、果蝇、蝗虫等作为研究相应导航神经机制的模式[58,59].

4.2 研究难点

(ⅰ) 感受器是否存在． 虽然目前学术界普遍接受磁导航存在磁铁石和化学感受两种机制，但是感受器的功能仍有待验证．Treiber等人[60]证实家鸽上

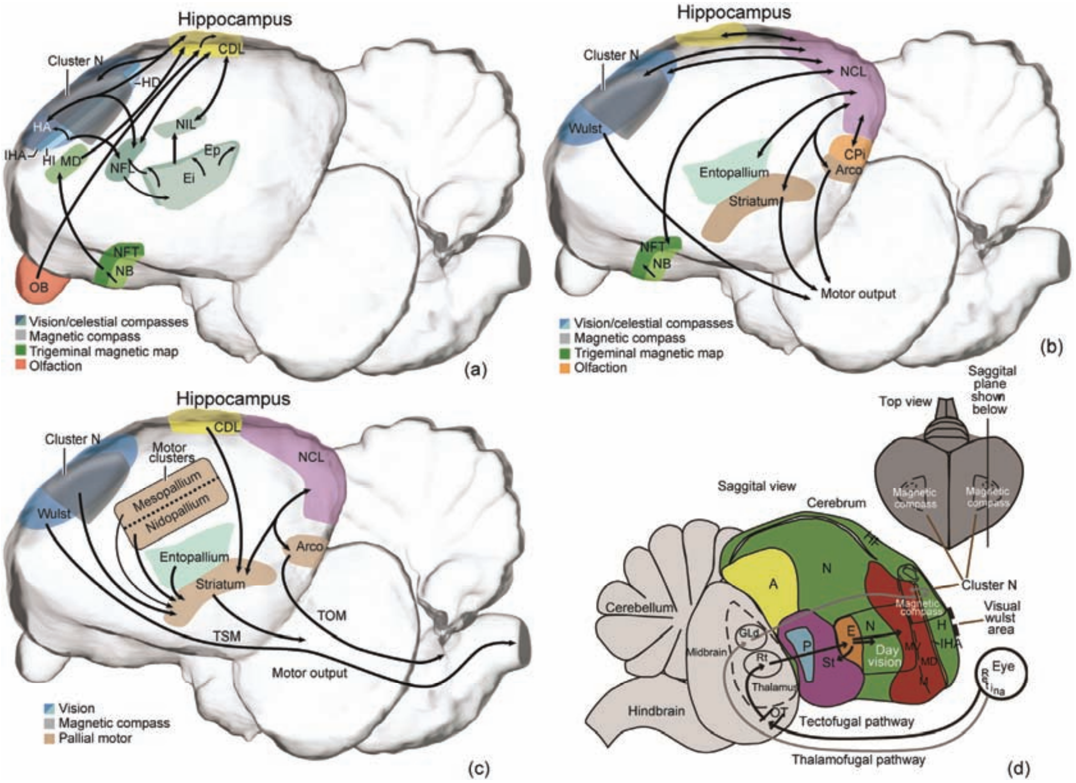

图 6 (网络版彩色)不同神经区域与神经通路共同协作控制导航[25,38]. (a) 储存、整合、重现地图和指南的海马通路; (b) 控制导航的各脑区将信息传入NCL通路; (c) 大脑动力输出路径; (d) 各导航神经机制综合

Figure 6 (Color online) Different neural regions and circuits control navigation together[25,38]. (a) Hippocampus region and pathway to store, integrate, and retrieve information about maps and compasses; (b) navigation-relevant brain regions deliver information to NCL; (c) the motor output pathways in bird brain; (d) all brain regions and pathways about navigation

喙部的磁颗粒细胞是含铁沉淀的吞噬细胞, 不能产生磁场感受地磁强弱. 果蝇全基因组筛查中发现一种磁受体(magnetoreceptors, MagR), 能与CRY形成多聚磁感受复合物, 具有两极指南特征, 能直接感受地磁信息[61]. 但MagR是否参与磁铁石和化学感受过程, 使两种机制偶联进行磁导航, 尚待验证.

(ⅱ) 自由基对反应. 光依赖自由基对反应是化学感受假说的理论基础. 自由基对在自旋单态和三态间的转换受到电子和原子核的超耦合的影响, 但是超耦合是如何影响的, 以及自由基对单态与三态的具体转换过程并不清楚. 在较潮湿、温度较高的体内这些量子过程是如何发生, 量子相干怎样才能持续较长时间及其维持长时间的物理机制、磁场放大机制等, 仍有待进一步研究[7,62,63].

(ⅲ) 神经回路与认知学习. 鸟类大脑各感受区域在结构上的连接已经很清楚, 但是在功能上的联系, 尤其是特殊感觉信息和导航定向的认知与决策等方面的研究还很滞后. 目前迁徙鸟类导航在神经回路与认知方面存在以下主要问题[64,65]: 鸟类在迁徙期与非迁徙期的行为转变及其神经机制; 幼鸟迁徙过程中, 遗传因素与外部信号之间在时空控制上的作用; 不同导航线索在神经网络中的决策及其重要性; MagR与CRY复合物的神经通路及大脑功能区; 迁徙鸟类与非迁徙鸟类大脑的特异性或指令的区别; 初期迁徙的学习对以后迁徙的影响, 以及导航与鸟类年龄和发育阶段的关系; 定向和导航机制对迁徙路线的影响及其神经机制; 大脑认知在迁徙鸟类中对形成新迁徙路线的作用, 以及影响新迁徙路线形成的可能性和限制因素.

4.3 环境、生态因子的综合影响因素

鸟类迁徙是一个漫长而艰辛的过程. 鸟类不但在迁徙之前需要积聚能量等一系列生理准备, 而且在迁徙途中需要面临温度、气压、风速、洋流等气候变化以及天敌和人为活动影响等多种外界因素. 这些都会对鸟类迁徙产生重要的影响, 在其迁徙机理

研究中应予以综合考量. 未来的发展, 只有综合考虑鸟类在迁徙过程中自身生理、生态、行为等内禀因素以及外界环境的影响作用, 才能够更好地回答迁徙鸟类是如何发现其迁移路线的问题.

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Summary for “迁徙鸟类如何发现其迁移路线?”

How do migrating birds find their way?

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Bird is one of the most abundant and widespread groups in the world. With many specialized structures, such as plumage, air sacs, and hollow bones, most bird species have got flight ability to adapt various niches. Therefore, bird can migrate between wintering and breeding ground, which is usually a long distance, and it’s called migration. Bird navigation is important in migration and is a complex process, which attracts many scientists to dig in how bird finds its way. Since 1873, Charles Darwin has ever mentioned that bird might take the method of dead reckoning on a long-distance migration like human, but at that time no one made further progress. Until 1950s, Kramer firstly found that Common Starling (*Sturnus vulgaris*) can respond to solar azimuth via mirror test. From then on, many experiments revealed that at least four navigation mechanisms are used in bird migration via more than nine external factors. They are: (i) celestial navigation, celestial clues (e.g. solar azimuth, star position, and polarized light) are used during migration period. (ii) Olfactory navigation, odor distributing in the air forms odorous gradient map or mosaic map which can be detected, or can activate directly certain mechanism to navigate. (iii) Auditory navigation, infrasound (0.05 Hz) produced by mountains and rivers generate sonic gradient map. And (iv) magnetic navigation, geomagnetic field can be detected via magnetic materials or chemical magnetoreception to find correct directions. Although many scientists approve that magnetic navigation may be the main mechanism to orientate and navigate, bird has never taken just one mechanism to migrate. Indeed, many species also use the other three mechanisms to calibrate direction, for example, Savannah Sparrow (*Passerculus sandwichensis*) can use polarized light to calibrate the magnetic compass at both sunrise and sunset. Different external clues correspond to different sense organs, so various brain areas should deal with information from different navigation mechanisms. The hippocampus participates in spatial perception and manages anything about celestial navigation via the tectofugal visual pathway and the thalamofugal visual pathway. The piriform cortex (CPi) is the main area to receive stimulation from olfactory bulb and determines how to migrate after receiving olfactory clues. Nervous systems of magnetic navigation include two parts which are trigeminus system and Cluster N. Despite the controversy whether there are some magnetic materials on bird, many experimental evidences have proved that magnetic materials detecting geomagnetic field involve to Trigeminus system. Cluster N, however, is an active area when bird migrates at night and it has an important role in transferring information from chemical magnetoreception to the hippocampus. As illustrated above, navigation mechanisms can get full information from many clues, and then, different brain areas trade off those and co-operate each other to make an elaborate map. Bird navigation involves the receptors to environment and the response of nervous system, so many issues are still maintained. The exact mechanism will be revealed with the new techniques and model animal applied.

migrating birds, celestial navigation, olfactory navigation, auditory navigation, magnetic navigation, neuromechanism

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