A bird's eye view of the hippocampus beyond space: Behavioral, neuroanatomical, and neuroendocrine perspectives

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ABSTRACT

Although the hippocampus is one of the most-studied brain regions in mammals, research on the avian hippocampus has been more limited in scope. It is generally agreed that the hippocampus is an ancient feature of the amniote brain, and therefore homologous between the two lineages. Because birds and mammals are evolutionarily not very closely related, any shared anatomy is likely to be crucial for shared functions of their hippocampi. These functions, in turn, are likely to be essential if they have been conserved for over 300 million years. Therefore, research on the avian hippocampus can help us understand how this brain region evolved and how it has changed over evolutionary time. Further, there is a strong research foundation in birds on hippocampal-supported behaviors such as spatial navigation, food caching, and brood parasitism that scientists can build upon to better understand how hippocampal anatomy, network circuitry, endocrinology, and physiology can help control these behaviors. In this review, we summarize our current understanding of the avian hippocampus in spatial cognition as well as in regulating anxiety, approach-avoidance behavior, and stress responses. Although there are still some questions about the exact number of subdivisions in the avian hippocampus and how that might vary in different avian families, there is intriguing evidence that the avian hippocampus might have complementary functional profiles along the rostral-caudal axis similar to the dorsal-ventral axis of the rodent hippocampus, where the rostral/dorsal hippocampus is more involved in cognitive processes like spatial learning and the caudal/ventral hippocampus regulates emotional states, anxiety, and the stress response. Future research should focus on elucidating the cellular and molecular mechanisms – including endocrinological - in the avian hippocampus that underlie behaviors such as spatial navigation, spatial memory, and anxiety-related behaviors, and in so doing, resolve outstanding questions about avian hippocampal function and organization.

1. Introduction

In mammals, the hippocampus - so named because the human version looks vaguely like a seahorse - is "one of the most thoroughly investigated structures in the brain" (Knierim, 2015), playing a critical role in memory formation, spatial representation, anxiety, and stress. In fact, many foundational neurobiological processes and patterns were first worked out in the mammalian hippocampus. Long-term potentiation, where synapses are strengthened from recent activity, is now considered one of the major cellular mechanisms underlying learning and memory (Morris, 2003), and was discovered in rabbit hippocampus by Bliss and Lømo (1973). Adult neurogenesis was first discovered by

Altman and Das (1965) and Kaplan and Hinds (1977) in the rat hippocampus, although it did not achieve scientific consensus until it was shown more broadly within the avian song system by Nottebohm and colleagues (Burd and Nottebohm, 1985; Goldman and Nottebohm, 1983; Paton and Nottebohm, 1984). The hippocampus is arguably best known for its arrays of place cells, discovered in rat hippocampus by O'Keefe and Dostrovsky (1971), which, together with head direction cells and grid cells found in other, connected brain regions, form a cognitive "map" of the spatial environment. However, once one moves beyond mammals, the number of papers related to – and our subsequent understanding of – the vertebrate hippocampus drops off dramatically, despite the fact that there is strong evidence that the hippocampus and

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at least some of its functions are conserved across vertebrate taxa (Colombo and Broadbent, 2000; O'Connell and Hofmann, 2011; Striedter, 2016; Witter et al., 2017). In this review, our goal is to summarize our current understanding of the avian hippocampus. Critically, although we begin by discussing the avian hippocampus's role in spatial cognition, we seek a broader understanding of the hippocampus "beyond space," which includes its essential role in regulating anxiety and stress responses; a role that is sometimes overlooked, especially in non-mammalian systems.

Many of us who work in comparative model systems (a politely scientific way to say "weird animals") are used to some version of the question "why study [your question] in [your weird animal]?" So let us get right down to it. There are really two main reasons to study the hippocampus in birds. The first is that understanding the hippocampus homologue in a non-mammalian vertebrate group with a complex brain and distinct evolutionary history can help us more broadly understand "what a hippocampus is for and how it works." Because birds and mammals are evolutionarily not very closely related, any shared anatomy and functions of their hippocampi are probably ancestral, which can help us understand how this brain region evolved and how it has changed over time. Comparing the hippocampus between birds and mammals (and beyond, to other vertebrate taxa) may also elucidate the relationship between hippocampus form and function from the view of comparative neuroanatomy and neural circuitry. For example, many computational models have been developed to explain hippocampal function based on the specific connectivity patterns of the mammalian hippocampus (e.g., Azizi et al., 2013; Lörincz and Buzsáki, 2000; Witter, 2018). Often, the assumption is that such architecture is the only way to achieve a particular function. The avian hippocampus allows us to test this assumption: if the avian hippocampus uses similar architecture to solve the same problem, this is probably evolutionarily conserved, and supports the assumption. If, on the other hand, the avian hippocampus can implement the same function with a different architecture, it means there are multiple ways for brains to link structure to a given function. As another example of the value of the comparative approach, the enzyme aromatase, which converts androgens to estrogens, has been found in the hippocampus or a hippocampus-like region (the reptile medial cortex and fish dorsolateral telencephalon) of many vertebrates (Azcoitia et al., 2011; Forlano et al., 2001; Krohmer et al., 2002; Peterson et al., 2005; Yague et al., 2008), suggesting that local estrogen production is necessary to support the cognitive functions of this brain region across taxa (Vahaba and Remage-Healey, 2015).

The second reason to study the hippocampus in birds is from the perspective of diversity, rather than conserved evolutionary characteristics. Many avian species and families have fascinating, well-studied behavioral ecologies, with implications for neural function that may require hippocampal specializations. For example, thousands of different bird species undergo massive annual migrations, some of them across extraordinary distances. Many birds, such as small songbirds in the family Paridae, rely on their memory of stored caches of food to survive the winter. Avian species such as the brown-headed cowbird (*Molothrus ater*) are brood parasites, which must find and remember the location of heterospecific nests where they can lay their eggs to successfully breed. And indeed, the hippocampal formation is sometimes larger in migratory compared to non-migratory birds (Bingman and MacDougall-Shackleton, 2017; Healy et al., 1996; Pravosudov et al., 2006), in birds artificially selected for better navigation abilities (Rehkämper et al., 1988), in food-storing compared to non-food-storing birds (Krebs et al., 1989; Pravosudov and Clayton, 2002; Sherry et al., 1989), and in brood parasitic compared to non-parasitic birds (Clayton et al., 1997; Reboreda et al., 1996; Sherry et al., 1993).

However, the challenges of navigation, food caching, and brood parasitism are not always associated with increased hippocampus size (Healy et al., 1991), suggesting there may be other hippocampal specializations - or even other brain regions - that support these behaviors. There are also often nuances to these behaviors that make them more or less hippocampus dependent. For example, the hippocampus is more likely to help migrating birds navigate using familiar landscape features, and is less likely to be involved in navigating via olfaction, the sun, or a geomagnetic compass (Bingman and MacDougall-Shackleton, 2017); for more on this, see the section on the avian hippocampus and spatial cognition, below. There is also still much that is unknown about possible cellular and molecular mechanisms – including endocrinological – in the hippocampus, that support extraordinary avian behaviors like food caching and navigation (Bingman and Ewry, 2020). We believe this solid foundation of research in avian behavioral ecology, associated with a knowledge gap regarding specific mechanisms, creates exciting opportunities for scientists interested in exploring links between the brain, behavior, and evolution.

Now that we have hopefully convinced the reader that birds are a useful group to examine to understand both conserved and specialized functions of the hippocampus, we will next (very briefly) describe the anatomy of the hippocampus in mammals as a basis for comparison to avian hippocampal anatomy. In mammals, the hippocampus is a roughly cylindrical curved structure, which consists of two interlocking layers of neurons: the dentate gyrus and the hippocampus proper (also called the Ammon's horn) (Fig. 1A) (El-Falougy and Benuska, 2006). This interlocking organization is the same along the entire longitudinal axis of the mammalian hippocampus. The dentate gyrus receives major inputs from the entorhinal cortex (Chawla et al., 2005; Danielson et al., 2016; Jung and McNaughton, 1993) and is one of the primary sites of adult neurogenesis (Cameron and Gould, 1994; Eriksson et al., 1998; Gould et al., 1999). The hippocampus proper is made up of four regions called CA1, CA2, CA3, and CA4 ("CA" for "cornu Ammonis," Ammon's horn in Latin). The connectivity among these different regions is complex and still being discovered in more detail, and includes a trisynaptic circuit from the entorhinal cortex to the dentate gyrus, from there to CA3, then to CA1 and back to entorhinal cortex (Andersen, 1975), among many other connections. Additionally, there is evidence that different parts of the hippocampus along the longitudinal axis have different functions: the septal hippocampus (posterior in primates, dorsal in rodents), appears to be more involved in cognitive functions such as spatial memory, while the temporal hippocampus (anterior in primates and ventral in rodents) appears more related to stress, emotion, and affect (Fanselow and Dong, 2010). In humans, as well, recent work has supported a functional gradient along the anterior–posterior axis, where the anterior portion of the hippocampus appears more self-centric, associated with functions such as emotion and autobiographical memory, while the posterior hippocampus is more world-centric, associated with functions such as navigation and context processing (Plachti et al., 2019). Thus, the mammalian hippocampus can be thought of as pair of separate structures with a posterior/dorsal zone that appears to serve a "cold" cognitive function and an anterior/ventral zone that seems to serve a "hot" affective function. An intermediate region that has only partly overlapping characteristics with its neighbors separates the two.

2. Anatomy of the avian hippocampus

The avian hippocampus is located in the dorsomedial portion of the telencephalon, and has a very different structure than the mammalian hippocampus (Fig. 1B). Many different studies have attempted to identify avian hippocampal subdivisions; however, no clear consensus on the number of subdivisions has been reached. Early work in pigeon characterizing the hippocampal formation via Nissl staining described two subdivisions: the hippocampus proper and the parahippocampal area (the dorsal part of the medial wall between the hippocampal formation and the hyperpallium, formerly referred to as the accessory hyperstriatum (Karten and Hodos, 1967). In the 1990s, immunohistochemical markers were used to further delineate subdivisions of the pigeon hippocampus, revealing five subdivisions: a medial fiber tract extending dorsally, a dorsomedial area, a v-shaped area of large cells, and a ventral region including a ventromedial region between the arms of the v-
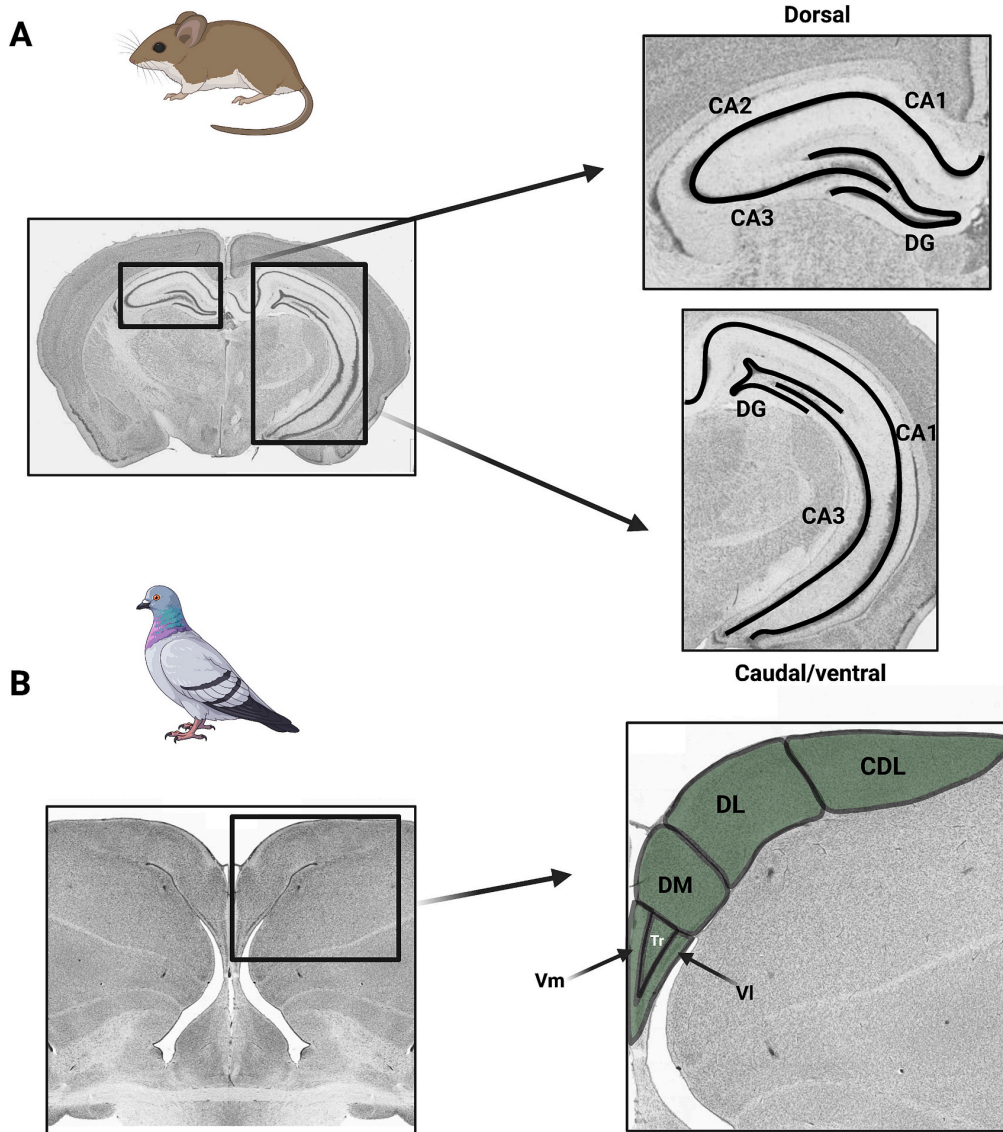
Fig. 1. Nissl-stained coronal sections of the brain (converted to grayscale) and schematic representations of the Peromyscus mouse dorsal and caudal/ventral hippocampus and pigeon hippocampal formation. **A:** Peromyscus dorsal and caudal/ventral Ammon's horn areas: CA1, CA2, CA3, and DG (dentate gyrus) **B:** Pigeon section through the rostral hippocampus. Within-section subdivisions are: dorsal medial (DM), dorsal lateral (DL), ventrolateral (Vl), ventromedial (Vm), cellular inner triangular region (Tr), dorsal lateral corticoid area (CDL). Peromyscus images from BrainMaps (accessed 28 July 2023), pigeon images courtesy of Christina Herold.

shaped area and the inferior part of the dorsomedial region (Erichsen et al., 1991). Additional immunohistochemical markers revealed subdivisions consistent with the four just described and revealed three additional subdivisions: a superior dorsomedial region, an area of diverse terminal fields in the medial dorsal region, and an area lateral and anterior to the hippocampal area (possibly outside the hippocampal area) (Erichsen et al., 1991; Krebs et al., 1991). To date, the number of subdivisions that have been described in pigeons (Atoji and Wild, 2004; Herold et al., 2014; Hough et al., 2002; Kahn et al., 2003), domestic chickens (Fujita et al., 2022; Gupta et al., 2012; Puelles et al., 2007; Suarez et al., 2006), and songbirds (Montagnese et al., 1996; Székely, 1999) vary both in nomenclature and proposed number. In songbirds such as the zebra finch, studies investigating the efferent connectivity of the dorsolateral, dorsomedial, and ventral regions revealed three subdivisions (Szekely and Krebs, 1996) while Montagnese et al. (1996) used

Nissl and zinc staining to describe five subdivisions: the area parahippocampalis, lateral and medial hippocampal layers, central field of the parahippocampus, and crescent field. This lack of consensus in the anatomy of avian hippocampal subdivisions can be a somewhat daunting barrier to researchers interested in studying this brain region.

Even when scientists can agree on how to subdivide the avian hippocampus, there is the additional challenge of trying to understand what regions may be homologous to structures found in the mammalian hippocampus. In the mammalian hippocampal formation, the dentate gyrus is described as a trilaminar, C-shaped region, most notably known to mediate functions such as learning and memory (Carpenter et al., 1976; Gall, 1990; Treves et al., 2008). As described above, the dentate gyrus serves as a link in the trisynaptic circuit relaying information from the entorhinal cortex to the dentate gyrus to CA3. Research suggests that while mammals evolved a dentate gyrus, the avian hippocampus may

have followed a different evolutionary path (Herold et al., 2019). Thus, the position, cytoarchitecture, and even existence of a dentate gyrus and Ammon's horn (specifically, CA1 and CA3) homologue in avian hippocampus is much debated (Striedter, 2016). Kahn et al. (2003) proposed a dentate gyrus homologue in pigeons in the dorsomedial hippocampus, while its location was described in the ventral region of the hippocampus by other authors examining pigeons and chickens (Atoji and Wild, 2004; Gupta et al., 2012; Puelles et al., 2007; Suarez et al., 2006). To further investigate possible correspondences between the avian hippocampus and mammalian dentate gyrus and CA regions, Herold et al. (2014) characterized the distribution of 11 neurotransmitter receptors and zinc expression in pigeons. They found similarities between the dentate gyrus/CA1 and the avian ventrolateral/triangular/ventro-dorsomedial regions, and some evidence that dorso-dorsomedial/ventromedial regions might be comparable to CA2/CA3. This work also revealed that the dorsolateral regions of the avian hippocampus seemed more comparable to the mammalian entorhinal cortex, a finding that has been further supported by anatomical and physiological studies of the dorsolateral hippocampus in food-caching songbirds (Applegate et al., 2023b). Further, attempts to identify a region of the avian hippocampus homologous to the well-defined granule cell layer and mossy fibers of the mammalian dentate gyrus failed to reveal a similar structure (Faber et al., 1989; Herold et al., 2014; Montagnese et al., 1996; Montagnese et al., 1993). Fiber-like projections have been observed in zebra finches (Montagnese et al., 1996), domestic chicks (Faber et al., 1989), and pigeons (Herold et al., 2014), yet the pattern of these fibers appears less organized than in the mammalian dentate gyrus. Thus, despite differences in structural anatomy, several studies have found some recognizable features of an "avian dentate gyrus"; however, more work is still necessary to verify its eventual structure and precise boundaries.

Although the avian hippocampus differs in structure compared to the mammalian hippocampus, the functional role of the hippocampus appears highly conserved across taxa (Bingman, 1993; Colombo and Broadbent, 2000). As described above, in mammals, the septal/dorsal/posterior region is more involved in spatial memory and the temporal/ventral/anterior region in responding to uncertain cues in the context of potentially threatening situations, including approach-avoidance decision making (Amadi et al., 2017; Ito and Lee, 2016; Vanni-Mercier et al., 2009) and negative feedback of the hypothalamic-pituitary-adrenal axis (de Kloet, 2008). The rostral portion of the avian hippocampus has been proposed to be equivalent to the rodent dorsal hippocampus, with the caudal portion of the avian hippocampus equivalent to the rodent ventral hippocampus (Smulders, 2017, 2021), suggesting these regions may be involved in similar functions to their mammalian counterparts. Like the rodent ventral hippocampus (Hawley and Leasure, 2012; Jayatissa et al., 2006; O'Leary and Cryan, 2014), the avian caudal hippocampus may be more sensitive to stress-induced decreases in adult neurogenesis (Armstrong et al., 2020b; Gualtieri et al., 2019; Herold et al., 2019), providing further support for it as a homologous subdivision to the ventral hippocampus.

The avian hippocampus receives extrinsic inputs from other pallial and thalamic regions that process sensory and at least geomagnetic compass information as well as regions important in emotionality, like the medial ventral arcopallium (AMV) (Heyers et al., 2022; Mello et al., 2019). In fact, retrograde tracing studies also support an organization of different functions along the long axis of the hippocampus, as the songbird rostral hippocampus receives more inputs from the thalamus and the caudal hippocampus receives more inputs from amygdalar regions (Applegate et al., 2023a). The hippocampus in turn sends projections back to other pallial regions as well as to septal and hypothalamic regions, including indirect connections to the paraventricular nucleus (PVN) (Smulders, 2021). Glucocorticoid receptors in brain regions such as the PVN and hippocampus regulate hypothalamic-pituitary axis activity and the cellular, physiological, and behavioral mechanisms that promote survival via the increased release of glucocorticoids (Fig. 2) (Krause et al., 2016; Krause et al., 2017; Landys et al.,
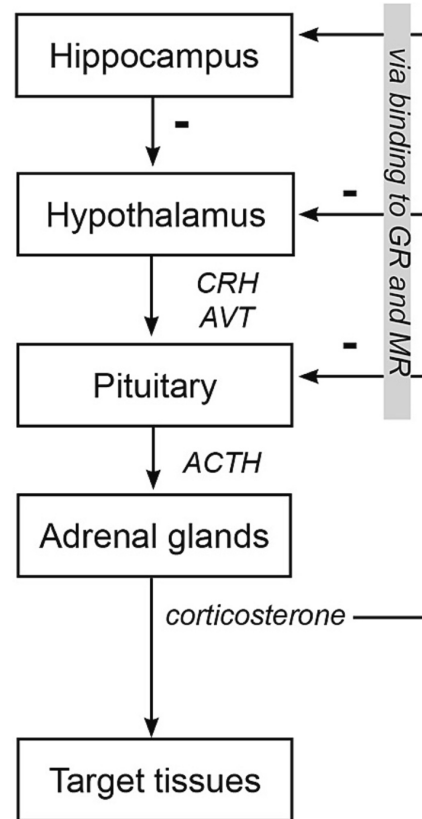

Fig. 2. In birds, the perception of a stressor causes the hippocampus to stimulate the paraventricular nucleus of the hypothalamus to release corticosterone releasing hormone (CRH) and arginine vasotocin (AVT), which travel to the pituitary gland via the hypophyseal portal system and stimulate the release of adrenocorticotropin hormone (ACTH). ACTH travels through the bloodstream to the adrenal cortex, where it causes the rapid synthesis and release of corticosterone. Corticosterone has various effects on target tissues throughout the body, and also feeds back to shut down its own release by binding to lower-affinity glucocorticoid receptors (GR) and higher-affinity mineralocorticoid receptors (MR) at the level of the hippocampus, hypothalamus, and pituitary.

2004). Corticosterone, the primary glucocorticoid released in birds and rodents, binds with high affinity to mineralocorticoid receptors (MR) under basal conditions while binding with lower affinity to glucocorticoid receptors (GR) under stressful conditions (Joels and de Kloet, 1994; Lattin et al., 2012; Romero, 2004). Both MR and GR are expressed in the avian and mammalian hippocampus (Baugh et al., 2017; de Kloet, 2014; Dickens et al., 2009; Hodgson et al., 2007; Joels et al., 2008; Krause et al., 2015; Lattin and Romero, 2013; Senft et al., 2016; Zimmer and Spencer, 2014), and are thought to play an important role in negative feedback of the hypothalamic-pituitary-adrenal axis in birds (Bouillé and Baylé, 1973) as in mammals (Jacobson and Sapolsky, 1991).

Finally, estrogen receptors, androgen receptors, and aromatase have been characterized in the avian hippocampus, as in the mammalian hippocampus (Gahr et al., 1993; Hodgson et al., 2008; Metzdorf et al., 1999; Saldanha et al., 1998). The presence of sex steroid receptors and aromatase in the avian hippocampus suggests local conversion of androgens to estrogens, and provides further support for conservation of the functional role of the hippocampus across mammals and birds (and, as mentioned above, to other vertebrate taxa such as reptiles and fish). Hippocampal aromatase has been found to be highly expressed in caching species, suggesting that local estrogen-dependent activity may be necessary to support memory for cache locations when circulating sex

steroid hormone concentrations are low (Saldanha et al., 1998). Moreover, inhibiting hippocampal estrogens by antagonizing aromatase with ATD (1,4,6-adrostatriene-2,17-dione), caused zebra finches to perform worse on spatial memory tasks, demonstrating the importance of aromatization for spatial memory performance (Bailey et al., 2013). Overall, the endocrine sensitivity and connectivity of the avian hippocampus reveals it to be a critical neural hub for the integration of sensory information with a bird's internal state to produce essential behaviors such as negotiating space (typically in three dimensions!) and responding to stressors.

3. The avian hippocampus and spatial cognition

3.1. The avian hippocampus and its canonical role in supporting the encoding of space

Any conversation about the functional profile of the avian hippocampus should probably begin with its role in spatial cognition, including its importance in supporting navigation and spatial memory. The discovery of hippocampal place cells in the mammalian hippocampus (O'Keefe and Dostrovsky, 1971), the theoretical developments of the hippocampus as a cognitive map (O'Keefe and Nadel, 1978), and the profound effect of mammalian hippocampal lesions on place navigation (Morris et al., 1982) inspired two seminal studies investigating whether the avian hippocampus was also important for spatial cognition. Bingman et al. (1984) tested the effects of hippocampal lesions on the ability of homing pigeons to navigate home from distant, unfamiliar release sites. They found that the ability of lesioned pigeons to orient homeward from release sites, and by implication the olfactory navigational map they used to determine the direction home from those distant sites (Gagliardo, 2013), was not impacted by the lesions. However, hippocampal-lesioned pigeons suffered a severe deficit in their ability to rely on familiar landmarks and landscape features to navigate closer to the home loft. Sherry and Vaccarino (1989) tested spatial memory for cache- and food-site locations in food-storing black-capped chickadees (*Poecile atricapillus*) that underwent hippocampal lesion and found that lesions disrupted birds' ability to recall the locations of stored or hidden seeds, while sparing their ability to discriminate food-site locations based on a distinctive local feature cue. Similar results were found some 20 years earlier in Eurasian nutcrackers (*Nucifraga caryocatactes*), but those results were essentially unknown outside of the Soviet Union (Krushinskaya, 1966). It is not an exaggeration to say that for almost 40 years since these papers were published, much of the research on the relationship between the avian hippocampus and spatial cognition has sought to provide a deeper understanding of these first findings (Herold et al., 2015).

3.2. Spatial memory

Research into the relationship between spatial memory, typically for food locations, and the hippocampus within the small-scale space of a lab is essentially a question about goal localization or recognition, i.e., "where is my goal within a local sensory domain?". This contrasts with field research, necessarily of a much larger spatial scale, which investigates the relationship between the hippocampus and navigational processes, i.e., "where am I and what is the path to my goal?" (see below). It is beyond the scope of this review to detail the impressive body of research that has accumulated regarding the relationship between the avian hippocampus and spatial memory (for reviews, see Pravosudov and Roth, 2013; Salwiczek et al., 2010; Sherry and Hoshooley, 2010; Smulders, 2006), but we would like to highlight what we think are some of the broader implications of the hippocampal-dependent memory work in birds.

For most food-storing birds, caching is a seasonal phenomenon, and it is associated with a seasonal upregulation of hippocampal neuron number, volume, and neurogenesis; for food-storing members of the *Paridae* this typically occurs in the fall (Barnea and Nottebohm, 1994; Lange et al., 2022; Sherry and Hoshooley, 2010; Sherry and MacDougall-Shackleton, 2015; Smulders et al., 1995; Smulders et al., 2000b); (but see Pravosudov, 2022). This seasonal variation in neurogenesis has naturally generated many questions on the control of that seasonal variation, and there is an emerging consensus that changes in photoperiod are not a direct cause. One alternative hypothesis is that the hippocampal volume responds directly to the amount of memory processing going on at those times of the year (Lange et al., 2022). What is often left unsaid, however, is that neurogenesis is a prominent feature in many regions of the avian telencephalon (Mehlhorn et al., 2022), and also occurs in the hippocampus of bird species that do not cache food, such as homing pigeons (Herold et al., 2019; Rook et al., 2023). In our view, there is increasing interest in the neuroanatomical properties of neurogenesis in the avian hippocampus. Associated with that interest is the goal of not only detailing the anatomy of neurogenesis, but also using those data to better understand the functional contribution of hippocampal neurogenesis to spatial memory, and offering insights into how variation in hippocampal *subdivisions* contribute to spatial cognition. For example, avian hippocampal neurogenesis is more prominent in anterior regions in pigeons (Herold et al., 2019) and wild black-capped chickadees (Barnea and Nottebohm, 1994), and it has been proposed that a higher resolution anatomical map of neurogenesis could help resolve the elusive question of whether there is a region equivalent to the mammalian dentate gyrus in the avian hippocampus (Herold et al., 2015; Rook et al., 2023).

Much has been made of the between-species differences in the importance of the hippocampal-dependent memory system in food-storing birds compared to non-food storing species (e.g., Brodbeck and Shettleworth, 1995; Clayton and Krebs, 1994; Hampton and Shettleworth, 1996), and even variation in the intensity of food-storing in different populations of the same species (Pravosudov and Clayton, 2002). The generalization that emerges from this work is that the hippocampal spatial memory system is hierarchically more important than more feature-based memory strategies in food-storing species compared to non-storing species, and more robust in more storing-dependent populations of the same species. However, this impression belies the reality that even in non-storing species, the hippocampal system can play a dominant role supporting memory for the spatial properties of a goal. For example, in non-food-storing zebra finches (*Taeniopygia guttata*) the hippocampus is essential for the spatial encoding of goal locations (Mayer and Bischof, 2012; Mayer et al., 2010), despite seemingly low levels of spatial stability in the response properties of their hippocampal neurons (Payne et al., 2021, see below). In homing pigeons, the spatial encoding of a goal location is also supported by the hippocampus, and similar to food-storing songbirds, hippocampal-dependent spatial encoding is often preferentially used over feature information (Bingman et al., 2006; Kahn and Bingman, 2009; Vargas et al., 2004). Indeed, the spatial response properties of homing pigeon hippocampal neurons seem to disproportionately represent goal locations (Bingman and Sharp, 2006; Hough and Bingman, 2004; Siegel et al., 2005). Even in taxonomically remote chickens, the hippocampus is instrumental for enabling the spatial encoding of goal locations (Morandi-Raikova and Mayer, 2021; Tommasi et al., 2003).

Inextricably bound to a discussion of the importance of the avian hippocampus for spatial memory is an understanding of the spatial response properties of single hippocampal neurons. The first generation of research into homing pigeon hippocampal neurons revealed a complex pattern of response properties that were clearly spatially modulated, but were different enough from the prototypical mammalian hippocampal place cell that the authors were reluctant to call them place cells (Bingman and Sharp, 2006; Hough and Bingman, 2004; Kahn et al., 2008; Siegel et al., 2005, 2006). A second generation of unit recording work examining species other than homing pigeons is now underway (Ben-Yishay et al., 2021; Payne et al., 2021; Takahashi et al., 2022). Notably, in contrast to the previous homing pigeon work (Kahn et al.,

2008), Payne et al. (2021) recorded from single hippocampal neurons in zebra finches and tufted titmice (*Baeolophus bicolor*) as the birds foraged for randomly dispersed food, and found place cells that very much resembled place cells recorded from rats. From a comparative-ecological perspective, it was especially interesting that what they defined as "place cells" were more abundant, stable, and spatially informative in the food-storing titmice compared to the non-storing zebra finches. However, what was left unexplored was how the spatial response properties of the neurons in titmice and zebra finches may have been modulated if a goal-memory component was part of the behavioral paradigm. Although not called place cells, place cell-like spatial responses are found in pigeon hippocampal neurons when stable goal locations, the recognition of which is reliant on memory, are placed in a test arena (Hough and Bingman, 2004; Siegel et al., 2005, 2006). Importantly, the profile of spatial response properties of hippocampal neurons in rats are also modulated by the presence of stable goal locations (e.g., Sosa and Giocomo, 2021).

3.3. Spatial navigation

The same avian hippocampus so important for spatial memory is similarly important in supporting navigation to goal locations; in other words, computing and executing a directed path from a start location to a remote goal location. In nature, birds engage in navigational movements that can vary considerably in scale, from local movements to known food, nesting or roosting sites that can range from tens of meters to several kilometers, to homing flights in homing pigeons and nesting seabirds that can reach a hundred or more kilometers, to the spectacular journeys of migratory birds that can be thousands of kilometers (Bingman and Cheng, 2005; Bingman and MacDougall-Shackleton, 2017). For homing pigeons, the hippocampus is important for navigation based on familiar landscape and landmark features—whether near the home loft or from more distant, familiar locations—when those landmark and landscape features are seemingly captured in a memory representation with properties that resemble a so-called cognitive map (Bingman et al., 2005; Gagliardo et al., 2009; Herold et al., 2015; O'Keefe and Nadel, 1978). Surprisingly, the hippocampus plays no necessary role in supporting the so-called navigational map of homing pigeons (Wallraff and Wallraff, 2005; Wiltschko and Wiltschko, 2003), which enables homeward orientation from distant, *unfamiliar* locations (Bingman et al., 1984; Bingman et al., 2005; Herold et al., 2015); it remains uncertain what role the hippocampus may play in supporting the long-distance navigation of migratory birds (Bingman and MacDougall-Shackleton, 2017).

3.4. A role in visual-spatial perception?

The dual roles of the avian hippocampus in recognizing the location of a goal and in navigation is conventionally thought to arise from a shared dependence on spatial memory, and the unit recording, lesion, and immediate early gene research described above is certainly consistent with such an interpretation. However, some recent research exploiting the high spatial resolution tracking of homing pigeon flights paths with GPS-recording devices have yielded data challenging the seemingly settled issue that the hippocampus is substantially about memory (for other studies challenging this memory-centric view, see work showing deficits in autoshaping and behavioral inhibition in hippocampal-lesioned pigeons (Johnston et al., 2020; Scarf et al., 2014)). Gagliardo et al. (2009) did not discuss in any detail the curious finding that many of their hippocampal-lesioned birds, but none of their control pigeons, flew out over the sea during their experimentally manipulated flight paths home. However, that neglected observation took on new meaning with the discovery that during their flights home from distant *unfamiliar* release sites, hippocampal-lesioned pigeons were more likely to take a straighter path home compared to controls. This straighter flight path was interpreted to reflect a visual-spatial *perceptual*

or attentional deficit (Gagliardo et al., 2014; Herold et al., 2015), with the hippocampal-lesioned birds flying out over the sea now thought to be a consequence of a perceptual/attentional impairment: a failure to recognize the landscape boundary between land and sea. Subsequently it was found that hippocampal-lesioned pigeons were less likely to develop fidelity to a particular route when repeatedly flying home from the same sites (Gagliardo et al., 2020), a route fidelity that would be dependent on the perception of and attention to visual landmarks and landscape features in addition to memory. Indeed, the route fidelity of the control pigeons was later found to rely in part on following landscape leading lines such as roads and woodland margins, and in that study, it was also observed that hippocampal-lesioned pigeons were more likely to display high frequency, oscillatory shifts in their flight paths, suggesting that they were casting about for presumably visual information (Gagliardo et al., 2023). We acknowledge that any one of the above-cited studies may not by itself offer a compelling reason to challenge the canonical memory interpretation of avian hippocampal function. However, we believe that collectively the data render more than just speculative the hypothesis that the avian hippocampus participates in the perceptual or attentional control of vision in the context of constructing integrated spatial scenes of landscapes; landscape scenes they fly through when returning home. Notable here is that conversations about hippocampal function in mammals, particularly in humans that share with birds a strong dependence on vision in constructing a perceptual moment, have expanded to include a role for the hippocampus in visual perception (e.g., Nau et al., 2018; Zeidman et al., 2015). We look forward to future experiments that rely on laboratory controls to determine whether, and perhaps eventually how, the avian hippocampus influences visual-spatial perceptual and attentional processes.

3.5. "Value" maps?

Further complicating a simple, spatial memory-centric functional characterization of the avian hippocampus is a growing recognition that the mammalian hippocampus—particularly more ventral regions, in the case of the rat hippocampus—integrates spatial information with event or valence properties, i.e., the extent to which good or bad things happen at particular locations in space (Jeong et al., 2018; Jin and Lee, 2021; Jung et al., 2018; Mizumori and Tryon, 2015; Sosa and Giocomo, 2021). Therefore, a revisionist label of a hippocampal-dependent "cognitive-value map" may not be inappropriate. Two recent papers suggest that the reward modulation of the mammalian hippocampus is in part explained by dopaminergic inputs from the ventral tegmental area (VTA) (Elliott et al., 2022; Krishnan et al., 2022). It is noteworthy, therefore, that a similar VTA to hippocampus projection is found in birds (Casini et al., 1986), the avian hippocampus too receives dopaminergic input (Herold et al., 2014; Krebs et al., 1991), and as described above, homing pigeon hippocampal neurons are disproportionately more likely to display fields of higher firing rates at reward-goal locations (Hough and Bingman, 2004; Siegel et al., 2005, 2006).

At the behavioral level, the first indication that the avian hippocampus supports the integrated representation of reward outcomes with locations in space was the observation that hippocampal-lesioned homing pigeons could encode the location of rewarded goal locations but could not distinguish which reward location was associated with a particular landmark-array context (White et al., 2002). Although this result has been framed as failed pattern separation (Herold et al., 2015), it is nonetheless suggestive of some hippocampal-dependent interaction between space and the events that occur at specific locations. More curious are the results of Kahn and Bingman (2009) demonstrating that hippocampal-lesioned pigeons could remember the locations of food-reward sites but could not differentially represent the variation in the reward quality of those locations (Fig. 3). By contrast, the ability to represent variation in the quality of reward associated with different food-bowl color features was not impacted by hippocampal lesion
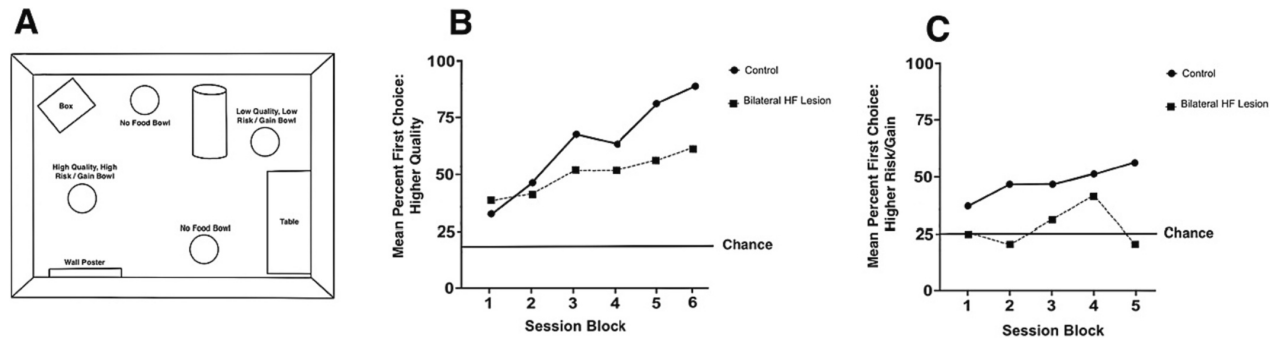
Fig. 3. Hippocampal formation (HF) lesions impact value assessment/risk associated with spatial location. **A.** In the two studies described, variations of the depicted experimental arena were used. The generalized arena is characterized by spatial polarizing cues and food bowls, some of which never contain a reward and two of which contain rewards of higher quality/value food or lower quality/value food. **B.** Control pigeons quickly learn to direct their first choices of a trial to a food bowl of higher quality (more preferred food item), while HF-lesioned pigeons display less of a preference and continue to choose equally between the food bowl of high and low (less preferred food item, data not shown) quality. See Kahn and Bingman (2009) for details. **C.** Control pigeons rapidly learn to direct their first choices of a trial to a food bowl that contains five seeds in 75 % of trials (zero seeds in 25 %), the food bowl of higher long-term gain but higher risk on any one trial, compared to a food bowl that contains two seeds in 100 % of trials. By contrast, HF-lesioned pigeons show no increasing preference for the higher risk bowl, preferring the two seeds in the no risk, constant food-reward bowl (data not shown). See Sizemore et al. (2022) for details. Although the two studies differ considerably with respect to the behavioral demands of the task, the data from both are consistent with HF-lesions impairing homing pigeons in integrating a map-like, spatial representation of goal locations with differences in the "value" associated with those goal locations.

(Coppola et al., 2014). Most compellingly, hippocampal lesions resulted in homing pigeons seemingly becoming more risk averse, displaying a stronger preference for a location with a small, certain reward compared to another location that contained a larger reward that was only periodically baited but which, long-term, would yield more food; intact pigeons more strongly preferred the larger but less predictable reward site (Sizemore et al., 2022). Taken together, the neuroanatomy, neurochemistry, neuronal spatial response properties and lesion work suggest a functional profile of the avian hippocampus that goes beyond a neutral, cognitive map-like representation of space to include something like a distortion in the representation of space that captures in memory the salience or valence of differential reward outcomes.

4. The avian hippocampus and anxiety, approach-avoidance conflicts, and stress

Indeed, an involvement of the hippocampus in processing event valence is not completely surprising. While the mammalian hippocampus has been studied in the context of spatial navigation and memory for a long time, it has been studied in the context of emotional and stress-related behaviors for even longer, as part of the limbic or Papez circuit (Aggleton et al., 2022; El-Falougy and Benuska, 2006). Note that the mammalian hippocampus literatures on anxiety, approach-avoidance conflicts, and stress are somewhat distinct, but we do not see clear distinctions between these three types of functions in birds, and so we will address each in turn as part of a broader discussion of the affective functions of the avian hippocampus, where the hippocampus generally appears to be active when animals are stressed or anxious.

4.1. Anxiety

Several lines of research point to a role of the avian caudal hippocampus in anxiety, reminiscent of the anxiogenic role of dentate gyrus granule cells in the mouse ventral hippocampus (Anacker et al., 2018). In mice, newly-generated neurons in the ventral dentate gyrus inhibit the activity of these anxiogenic mature granule cells, making mice more resilient to the induction of anxiety by chronic stress treatments (Anacker et al., 2018). There is evidence that something similar may occur in birds as well. Japanese quail selected for long tonic immobility (i.e. high anxiety; Mills and Faure, 1991) had fewer newly-generated cells (probably neurons) in the hippocampus than birds selected for

short tonic immobility (Lormant et al., 2020). In Lormant et al. (2020)'s study, only relatively rostral sections were investigated, so it is unclear whether the link between anxiety and hippocampal neurogenesis is region-specific in quail as it is in mice. In contrast, laying hens that exhibited longer tonic immobility had higher expression of proliferating cell nuclear antigen (PCNA, indicative of more cell division) in both the rostral and caudal hippocampus (Armstrong et al., 2020b), a pattern that is consistent with a more reactive coping style (Lemaire et al., 1999). The results of these two studies are not necessarily incompatible, as one examined neuronal proliferation (hens) and the other survival of new neurons (quail). It is also possible that selection for increased tonic immobility affected different neural mechanisms than those involved in individual differences in coping style.

More evidence for responses to anxiogenic situations in the quail hippocampus comes from a study examining acute social isolation stress in 2–10 day old Japanese quail chicks. This treatment induced c-Fos reactivity especially in the dorsolateral area of the hippocampus, along the entire rostro-caudal extent (Takeuchi et al., 1996). Social isolation also strongly affected the hippocampal metabolome in broiler chicks, an effect that was partially mimicked by corticosterone treatment, but less so by heat stress (Brown et al., 2023). Anxiety-driven activation along the entire rostro-caudal extent of the hippocampus is also consistent with a study by Damphousse et al. (2022), who showed that neither rostral nor caudal hippocampal lesions impaired contextual fear conditioning. This kind of response would be dependent on the temporal (ventral) hippocampus in mammals. However, as this study did not use a group with complete hippocampal lesions, we do not know yet whether contextual fear conditioning requires the hippocampus at all in birds.

4.2. Approach-avoidance conflicts

Another type of anxiogenic situation involves approach-avoidance conflicts, situations where both positive and negative outcomes are possible and animals must balance their desire to seek reward with their desire to avoid harm. For example, foraging in an open environment may allow for increased food acquisition, but it can also make an animal more vulnerable to predation. Mammalian research has demonstrated a clear role for the hippocampus in resolving these conflicts to generate a binary behavioral outcome: "approach" or "avoid". In biomedical research, many different experimental paradigms are used to assess approach-avoidance conflicts, including some paradigms that rely on

the inherent rewarding properties of exploration for a "conflict" to exist, and others that pair reward with punishment, providing a clearer conflict that could potentially also involve fear circuitry (Bryant and Barker, 2020). Part of the interest in approach-avoidance behavior is the fundamental importance of being able to accurately perceive and weigh conflicting environmental information; in fact, inappropriate responses to approach-avoidance conflicts (approaching when it is safer to avoid, or avoiding when it is safe to approach) are one sign of neuropsychiatric illness (Calhoon and Tye, 2015; Gray and McNaughton, 2000; Russell, 1980). From an ecological and evolutionary perspective, many situations involve possible risk and reward for wild animals, and they must accurately weigh the two and act accordingly to maximize their fitness.

In rodent and human studies, approach-avoidance behavior is dramatically affected by hippocampal lesions (Bannerman et al., 2003; Gray and McNaughton, 2000; Pentkowski et al., 2006). When the hippocampus is lesioned, animals typically exhibit more approach-related behaviors; this lesion effect is similar to the effects of anxiolytic drugs (Gray, 1977; Rickels, 1978). This led to an early understanding that the hippocampus disproportionately weights negative stimuli; without a hippocampus, behavioral inhibition is suppressed, biasing behavior towards approach (Gray, 1982; Johnston et al., 2020; McNaughton and Gray, 2000). However, it is becoming more accepted that the mammalian hippocampus plays at least two different roles in approach-avoidance decision making (Bryant and Barker, 2020; Loh et al., 2017): first, it appears to monitor for conflicts between the desire to approach and the desire to avoid; second, it acts to inhibit behavior once a conflict is detected. These two functions can be collapsed into an understanding of the hippocampus as an arbitrator of conflicting stimuli.

Some recent work points to a similar role for the avian hippocampus in feeding neophobia trials where a novel object is paired with familiar food (Greenberg, 1990; Schaffer et al., 2021; Tobler and Sandell, 2007). Responses to feeding neophobia trials may represent a type of approach-avoidance behavior, where conflicting cues (positive stimulus of food, negative stimulus of novel objects) must be resolved by the brain (Bannerman et al., 2014; O'Neil et al., 2015). The first neophobia study used RNAseq to examine constitutive gene expression in four brain regions of house sparrows (*Passer domesticus*) that had been tested several weeks previously with different feeding neophobia paradigms (Lattin et al., 2022). The region showing the largest number of differentially expressed genes was the hippocampus, where 12 % of the transcriptome was significantly differentially expressed in neophobic and non-neophobic sparrows. Of note, the hippocampus sample in this study was located caudally in the brain. A second study exposed house sparrows to novel objects near the food dish, or just the normal food dish or no food dish as controls, and examined immediate early gene proteins in several brain regions (Kimball et al., 2022). This study found that novel objects near food, but not the two control treatments, were associated with a significant increase in c-Fos density in the caudal—but not rostral—hippocampus. These two studies demonstrate that the caudal hippocampus shows increased neuronal activity in response to novel objects in birds, as well as major differences in gene expression in individuals that typically choose to approach, rather than avoid, a food dish paired with a novel object. This is some of the best evidence we have thus far that the hippocampus may also be involved in approach-avoidance decision making in birds, although more experimental work manipulating hippocampal function is still necessary to verify this link. However, an earlier pigeon study does provide some evidence for such a causal link between the hippocampus and approach-avoidance decision making in birds. In this study, hippocampal-lesioned pigeons were more likely to ignore the presence of a human in the testing room, which paradoxically resulted in faster task shaping in lesioned birds (Broadbent and Colombo, 2000). All pigeons appeared to notice a human researcher behind a curtain, but the hippocampal-lesioned birds ignored the person and began searching for food, whereas control animals were more likely to freeze (M. Colombo, personal communication).

Passive Avoidance Learning is a long-used paradigm for studying one

trial learning in chicks, and involves another approach-avoidance conflict. Day-old chicks are presented with a bead to peck that is either covered in water or methyl anthranilate, which is very bitter. The chick learns to avoid the methyl anthranilate bead, but not the water-covered bead (Lee-Teng and Sherman, 1966). Pecking at the bitter bead is stressful and activates the hypothalamic-pituitary-adrenal (HPA) axis (Sandi and Rose, 1997), including an upregulation of cortisol in the hippocampus (Nikolakopoulou, 2005). This stressful event is accompanied by a reduced number of newly-generated cells in the hippocampus for the next 24 h, although these differences disappear by 9 days later (Nikolakopoulou et al., 2006b). There are also changes in the density of different types of synapses in different subdivisions of the hippocampus at various time periods post-exposure (Nikolakopoulou et al., 2006a; Unal et al., 2002). It remains to be elucidated which of these changes are a response to the stressful nature of the bitter bead, and which are related to the avoidance learning or indeed control of the avoidance itself. Pharmacological interventions of different subtypes of β adrenergic receptors and of NMDA receptors have shown that the hippocampus is necessary for the consolidation of this stress-induced memory (Gibbs et al., 2008), again linking hippocampal function to the association of event valence; in this case, to objects.

One limitation of most approach-avoidance paradigms is that they still contain significant spatial components, and, as described in detail above, the hippocampus plays a crucial role in representing spatial contexts. In fact, early work characterizing the hippocampus as part of the brain's broader behavioral inhibition system explicitly proposed that the hippocampus may act as a comparator between expected and actual environmental stimuli, which seems to require a prior spatial representation that does not match the current environment (Gray, 1982; Gray, 1987). The strongest evidence that the hippocampus plays a role in resolving approach-avoidance conflicts independent of mapping spatiotemporal information comes primarily from human studies using specially-designed tasks to hold spatiotemporal contexts constant while only changing the valence of task decisions (and, perhaps, changing the amount of anxiety experienced by participants). For example, when researchers used functional MRI to visualize brain activity during a gambling task that penalized wrong choices (an approach-avoidance conflict) versus a nearly identical task that only failed to reward wrong choices, they found evidence that the hippocampus was specifically recruited for avoidance behavior when a penalty was possible (Loh et al., 2017). This again is reminiscent of studies showing that the hippocampus is involved in linking (negative) valence information to spatial information, as discussed above (Jeong et al., 2018; Jin and Lee, 2021; Jung et al., 2018; Mizumori and Tryon, 2015; Sosa and Giocomo, 2021). The house sparrow feeding neophobia studies mentioned previously certainly contained a strong spatial element; in these studies, the food dish was always in the same place, and the novel objects represented an unexpected stimulus in this familiar feeding context (Kimball et al., 2022; Lattin et al., 2022). A different testing paradigm would be necessary to implicate the hippocampus in approach-avoidance behavior independent of its role in representing spatiotemporal information.

4.3. Chronic stress

Stress and anxiety are closely-linked concepts. Often, anxiety is triggered by stressful events (Korte et al., 2005; Smulders, 2017). It is therefore also useful to examine how the hippocampus responds to stress. The literature on the relationship between the mammalian hippocampus and stress is vast and will not be reviewed here (for more information, see e.g. Larosa and Wong, 2022; Ortiz and Conrad, 2018). Instead, we will focus on how the avian hippocampus responds to chronic stress and its role in regulating the stress response. For example, 24 h of food deprivation reduced the number of spines in the hippocampus of 15 and 30 day old chicks, with only one cell type showing an increase in spine density in 15-day old chicks (Kumar et al., 2023).

However, 24 h is not necessarily considered chronic stress. Much of the literature on chronic stress has focused on potential measures of adult hippocampal neurogenesis, rather than finer-scale changes like spine densities. Some studies used cell division markers, such as BrdU or ^{3}H-thymidine, while others used endogenous markers of immature neurons, like doublecortin (DCX). Although DCX is a reliable marker of new neurons in the rodent hippocampus (Brown et al., 2003; Rao and Shetty, 2004), it is still debated whether it solely marks new neurons in the avian brain (Balthazart and Ball, 2014a, 2014b; Vellema et al., 2014a; Vellema et al., 2014b), including the hippocampus.

A direct chronic stress manipulation (8 weeks of unpredictable chronic mild stress) reduced the density of DCX positive (DCX$^+$) neurons in the caudal (but not the rostral) pole of the hippocampus in young hens (Gualtieri et al., 2019). One of the major components of Gualtieri et al.'s unpredictable chronic mild stress was a disruption of the circadian rhythm. Wild Indian house crows (*Corvus splendens*) held for a week in individual small cages and then exposed to constant light (i.e., no dark phase) also had fewer DCX$^+$ neurons in the hippocampus compared to birds kept on a 12:12 L:D cycle (Taufique et al., 2018a). They also had smaller hippocampal neuronal somata and fewer hippocampal glia (Taufique et al., 2019). Dim light at night had similar effects, with depression-like behavioral symptoms accompanied by reduced DCX immunoreactivity, reduced Brain Derived Neurotrophic Factor (BDNF) immunoreactivity (another marker of plastic, possibly new neurons), and a decrease in the expression of several hippocampal genes, again including *bdnf* (Taufique et al., 2018b). These studies again demonstrate the sensitivity of the hippocampus to chronic stressors. However, the crow results stand in contrast to the effects of dim light at night in zebra finches: both male and female zebra finches bred in captivity and exposed to dim light at night had increased proliferation in the ventricular zone adjacent to the hippocampus, and increased recruitment and total neuron numbers in the hippocampus (Moaraf et al., 2021; Moaraf et al., 2020a; Moaraf et al., 2020b). The reasons for these different responses to dim light at night between Indian house crows and zebra finches are unclear, but could be related to the different neurogenesis markers used, the time spent on a dim light cycle, or species differences.

Several commercially-relevant stressors have also been shown to affect hippocampal neurogenesis (or at least DCX$^+$ cells numbers) in different chicken breeds. Chronic food restriction reduced the number of one-week-old newly-generated neurons in the hippocampus of 11-week-old broiler breeders, with effects observed in both rostral and caudal hippocampus (Robertson et al., 2017). Living with keel bone fractures (a common injury in commercial laying hens) reduced the density of DCX$^+$ neurons in the hippocampus of laying hens, also across both rostral and caudal poles. Hens that had lived with keel bone fractures for longer had further reduced DCX$^+$ densities in the caudal (but not the rostral) pole compared to birds that had acquired their keel bone fractures more recently (Armstrong et al., 2020a). Less extreme forms of chronic stress can also affect hippocampal plasticity. Laying hens in poor physical condition (possibly indicative of chronic stress) had lower DCX$^+$ densities across both rostral and caudal hippocampal poles than birds in good physical condition (Armstrong et al., 2022). Hens in poor physical condition are likely to be subordinate birds in the flock, and indeed, a similar effect was found in captive mountain chickadees (*Poecile gambeli*): subordinate birds had lower levels of cell proliferation in the hippocampal ventricular zone than dominant birds (Pravosudov and Omanska, 2005).

Bringing wild birds into captivity is itself a chronic stressor (reviewed by Phillmore et al., 2022), and this has been shown to reduce hippocampal volume in dark-eyed juncos (*Junco hyemalis*) (Smulders et al., 2000a), brown-headed cowbirds (*Molothrus ater*) (Day et al., 2008), mountain chickadees (LaDage et al., 2009), black-capped chickadees (Tarr et al., 2009), and house sparrows (Roth 2nd et al., 2017). In this last study, it was also shown that dendrite length of hippocampal neurons declined with captivity, as did dendritic spine density. Spine densities were clearly shown to be related to available space, as spine densities increased when birds were moved from smaller cages to larger aviaries after several months (Roth 2nd et al., 2017). Captivity also reduced hippocampal neurogenesis in black-capped chickadees when measured using ^{3}H thymidine (Barnea and Nottebohm, 1994) and in mountain chickadees when DCX was used (LaDage et al., 2010), but not when using BrdU as a cell division marker in black-capped chickadees (Tarr et al., 2009). Comparing hand-reared birds to wild-caught ones, it appears that the volume changes in the hippocampus, like the spine densities mentioned before, may be mostly due to a less enriched environment in captivity – that is, to impoverished spatial information processing. The reduction in DCX immunoreactivity may be more related to the stress of captivity, as DCX$^+$ densities are no different in hand-reared birds compared to wild birds, but are lower in wild-caught captive birds (LaDage et al., 2010; Roth et al., 2012);see also Smulders (2017) for a more complete argument.

4.4. Regulation of the stress response

The hippocampus' sensitivity to stress relates at least partially to its role in HPA axis negative feedback (Fig. 2). As mentioned earlier, the hippocampus is one of the few telencephalic brain areas that expresses both MR and GR (Cornelius et al., 2018; Dickens et al., 2011; Krause et al., 2015; Lattin and Romero, 2013; Senft et al., 2016; Shahbazi et al., 2011; Suzuki et al., 2011; Zimmer and Spencer, 2014). As MR have a higher affinity than GR for corticosterone, they are especially important in negative feedback at lower hormone titers (Jacobson and Sapolsky, 1991; Lattin et al., 2012). Tree swallows (*Tachycineta bicolor*) living in more extreme environments (Alaska vs. Wyoming and New York) have higher MR expression in the hippocampus (Zimmer et al., 2023). Chronic stress also induced higher levels of MR expression in the hippocampus in European starlings (*Sturnus vulgaris*) (Dickens et al., 2009). In contrast, zebra finches selected for high peak corticosterone responses to acute stressors had lower levels of MR expression than randomly-bred birds (Hodgson et al., 2007). Thus, it appears that chronically high levels of baseline corticosterone can lead to increases in MR (tree swallows and starlings), presumably to control these corticosterone levels. The down-regulation observed in zebra finches may be a protective response to regular high peak levels throughout life (Hodgson et al., 2007). None of the three species showed changes in hippocampal GR expression. However, breeding experience increased the number of GR in the pigeon hippocampus, which was associated with a reduced magnitude of the corticosterone responses to acute stress (Farrar et al., 2022). Experiencing acute stress did not change either MR or GR expression in the hippocampus of white-crowned sparrows (Krause et al., 2021). Overall, it is clear that MR and GR both play a role in controlling the HPA axis, albeit at different stages, with MR important at baseline levels, and GR at acute peak levels of corticosterone. The avian hippocampus also expresses receptors for corticotropin releasing hormone (CRH) (Gualtieri et al., 2019). Levels of CRHR1 are lower in domesticated chickens than in red jungle fowl, showing that domestication can also affect hippocampal involvement in the stress response (Lotvedt et al., 2017).

The role of the avian hippocampus in HPA axis negative feedback was thoroughly explored in a suite of studies in the 1970s (summarized in Smulders, 2017, 2021). These studies showed that the pigeon hippocampus has an inhibitory influence on the HPA axis, probably as part of the mechanism that brings HPA axis activity back down to baseline after an acute stressor, as it does in mammals (Ulrich-Lai and Herman, 2009). Hippocampal lesions eliminated the circadian rhythm in corticosterone titers by raising them to peak levels at all times, and removal of the entire telencephalon (including the hippocampus) delayed the return to baseline of corticosterone after an acute stressor (Ramade et al., 1979). Hippocampal inhibition of the HPA axis works through inhibition of hypothalamic activity (Bouille and Bayle, 1976, 1978). Stimulation of the hippocampus, especially at more caudal levels, suppressed corticosterone concentrations. The anatomical route through

which the hippocampus influences the HPA axis is still only partially understood. There is some evidence for direct connections from subdivisions of the hippocampus either directly to the paraventricular nucleus of the hypothalamus (PVN; the hypothalamic "top" of the HPA axis) (Atoji and Wild, 2004; Herold et al., 2019; Szekely and Krebs, 1996), or to its axons projecting to the median eminence (Bons et al., 1976). The evidence is stronger for indirect projections via the septum (Atoji and Wild, 2004; Herold et al., 2019), lateral hypothalamus (Atoji and Wild, 2004; Casini et al., 1986; Felix and Roesch, 1984), and the lateral bed nucleus of the stria terminalis (Atoji et al., 2006; Atoji et al., 2002), among others. However, the exact pathway has not yet been determined. For a detailed review of these connections, see Smulders (2021).

5. Conclusions

Despite major anatomical differences, the role of the hippocampus in the control of spatial cognition, anxiety, and chronic stress appears well conserved across birds and mammals, and there are also conserved neuroendocrine mechanisms across taxa, such as the involvement of hippocampal GR and MR in mediating stress responses. More work needs to be done to better understand the role of the hippocampus in acute stress responses, and to clarify to what extent approach-avoidance responses can be separated from their spatial contexts. Future research should also focus on elucidating the cellular and molecular mechanisms in the avian hippocampus that underlie behaviors such as spatial navigation, food caching, and anxiety-related behaviors. Overall, the shared functional profile of the hippocampus between birds and mammals reveals that a hippocampus does not have to be "built" like the mammalian hippocampus to influence the above-mentioned functions. Which hippocampal functions are ancestral, versus which functions may have arisen via convergent evolution, would be clarified by further study of the hippocampus in sister taxa to birds, like crocodilians, or in more distant, similarly related taxa, such as fish.

Unfortunately, the avian hippocampal literature, just like the mammalian literature, is somewhat siloed based on function; that is, there is a "stress and the hippocampus" literature, a "spatial cognition and the hippocampus" literature, etc., with little intellectual cross talk between them. It is not clear to us whether there is a "grand unifying theory" of the hippocampus that might be able to unify all these functions, but at the very least, it is useful for researchers working on the hippocampus to be aware of what is going on in the other silos! It is also possible that part of the reason for these silos is that there is not just one hippocampus, but an anatomical-functional heterogeneity, which appears to be another similarity between birds and mammals. The role of the hippocampus in spatial cognition is more readily localized to one pole (in birds, this is the rostral hippocampus; in mammals, this is the dorsal/posterior/septal region), with stress, avoidance, and anxiety functions more readily localized to the other pole (in birds, this is the caudal hippocampus; in mammals, it is the ventral/anterior/temporal region). This rostral-caudal "functional axis" of the avian hippocampus is still somewhat unresolved, however, and merits further examination. It also is somewhat unclear how much this proposed division is built into the structure, physiology, and connectivity of the avian hippocampus itself, and to what extent, if any, this separation overlaps with any of the previously proposed subregions of the hippocampus.

What is clear, however, is that the avian hippocampus is not a brain region that we have completely figured out yet. Recent studies of the avian brain have used molecular approaches examining dozens of different genes in many different brain regions to reveal exciting new patterns, such as a mirror image profile of pallial gene expression above and below the lateral ventricle, and a columnar-like pallial organization that may impact motor and sensory processing (Gedman et al., 2021; Jarvis et al., 2013; Stacho et al., 2020). A broad molecular approach would be useful to apply to the avian hippocampus as well, to help resolve its organization (for example, settling the question of whether

there is actually an "avian dentate gyrus") and to provide further evidence for or against a rostral-caudal organization. A better understanding of hippocampal organization would help guide future research on a critical brain region that does more than help birds remember useful locations, but also adds valence and value to their understanding of the world.

References

Aggleton, J.P., Nelson, A.J.D., O'Mara, S.M., 2022. Time to retire the serial Papez circuit: implications for space, memory, and attention. Neurosci. Biobehav. Rev. 140, 104813.

Altman, J., Das, G.D., 1965. Autoradiographic and histological evidence of postnatal hippocampal neurogenesis in rats. J. Comp. Neurol. 124, 319–335.

Amadi, U., Lim, S.H., Liu, E., Baratta, M.V., Goosens, K.A., 2017. Hippocampal processing of ambiguity enhances fear memory. Psychol. Sci. 28, 143–161.

Anacker, C., Luna, V.M., Stevens, G.S., Millette, A., Shores, R., Jimenez, J.C., Chen, B., Hen, R., 2018. Hippocampal neurogenesis confers stress resilience by inhibiting the ventral dentate gyrus. Nature 559, 98–102.

Andersen, P., 1975. Organization of hippocampal neurons and their interconnections. In: The Hippocampus: Volume 1: Structure and Development, pp. 155–175.

Applegate, M.C., Gutnichenko, K.S., Aronov, D., 2023a. Topography of inputs into the hippocampal formation of a food-caching bird. J. Comp. Neurol. 531, 1669–1688.

Applegate, M.C., Gutnichenko, K.S., Mackevicius, E.L., Aronov, D., 2023b. An entorhinal-like region in food-caching birds. Curr. Biol. 33, 2465–2477.e2467.

Armstrong, E.A., Rufener, C., Toscano, M.J., Eastham, J.E., Guy, J.H., Sandilands, V., Boswell, T., Smulders, T.V., 2020a. Keel bone fractures induce a depressive-like state in laying hens. Sci. Rep. 10, 3007.

Armstrong, E.A., Voelkl, B., Voegeli, S., Gebhardt-Henrich, S.G., Guy, J.H., Sandilands, V., Boswell, T., Toscano, M.J., Smulders, T.V., 2020b. Cell proliferation in the adult chicken hippocampus correlates with individual differences in time spent in outdoor areas and tonic immobility. Front. Vet. Sci. 7.

Armstrong, E.A., Richards-Rios, P., Addison, L., Sandilands, V., Guy, J.H., Wigley, P., Boswell, T., Smulders, T.V., 2022. Poor body condition is associated with lower hippocampal plasticity and higher gut methanogen abundance in adult laying hens from two housing systems. Sci. Rep. 12, 15505.

Atoji, Y., Wild, J.M., 2004. Fiber connections of the hippocampal formation and septum and subdivisions of the hippocampal formation in the pigeon as revealed by tract tracing and kainic acid lesions. J. Comp. Neurol. 475, 426–461.

Atoji, Y., Wild, J.M., Yamamoto, Y., Suzuki, Y., 2002. Intratelencephalic connections of the hippocampus in pigeons (Columba livia). J. Comp. Neurol. 447, 177–199.

Atoji, Y., Saito, S., Wild, J.M., 2006. Fiber connections of the compact division of the posterior pallial amygdala and lateral part of the bed nucleus of the stria terminalis in the pigeon (Columba livia). J. Comp. Neurol. 499, 161–182.

Azcoitia, I., Yague, J.G., Garcia-Segura, L.M., 2011. Estradiol synthesis within the human brain. Neuroscience 191, 139–147.

Azizi, A.H., Wiskott, L., Cheng, S., 2013. A computational model for preplay in the hippocampus. Front. Comput. Neurosci. 7, 161.

Bailey, D.J., Ma, C., Soma, K.K., Saldanha, C.J., 2013. Inhibition of hippocampal aromatization impairs spatial memory performance in a male songbird. Endocrinology 154, 4707–4714.

Balthazart, J., Ball, G.F., 2014a. Doublecortin is a highly valuable endogenous marker of adult neurogenesis in canaries. Brain Behav. Evol. 84, 1–4.

Balthazart, J., Ball, G.F., 2014b. Endogenous versus exogenous markers of adult neurogenesis in canaries and other birds: advantages and disadvantages. J. Comp. Neurol. 522, 4100–4120.

Bannerman, D., Grubb, M., Deacon, R., Yee, B., Feldon, J., Rawlins, J., 2003. Ventral hippocampal lesions affect anxiety but not spatial learning. Behav. Brain Res. 139, 197–213.

Bannerman, D.M., Sprengel, R., Sanderson, D.J., McHugh, S.B., Rawlins, J.N.P., Monyer, H., Seeburg, P.H., 2014. Hippocampal synaptic plasticity, spatial memory and anxiety. Nat. Rev. Neurosci. 15, 181–192.

Barnea, A., Nottebohm, F., 1994. Seasonal recruitment of hippocampal neurons in adult free-ranging black-capped chickadees. Proc. Natl. Acad. Sci. U. S. A. 91, 11217–11221.

Baugh, A.T., Senft, R.A., Firke, M., Lauder, A., Schroeder, J., Meddle, S.L., van Oers, K., Hau, M., 2017. Risk-averse personalities have a systemically potentiated neuroendocrine stress axis: a multilevel experiment in Parus major. Horm. Behav. 93, 99–108.

Ben-Yishay, E., Krivoruchko, K., Ron, S., Ulanovsky, N., Derdikman, D., Gutfreund, Y., 2021. Directional tuning in the hippocampal formation of birds. Curr. Biol. 31 (2592–2602), e2594.

Bingman, V.P., 1993. Vision, cognition and the avian hippocampus. In: Ziegler, H.P., Bischoff, H.-J. (Eds.), Vision, Brain, and Behaviour in Birds. MIT, Cambridge, MA, pp. 391–408.

Bingman, V.P., Cheng, K., 2005. Mechanisms of animal global navigation: comparative perspectives and enduring challenges. Ethol. Ecol. Evol. 17, 295–318.

Bingman, V.P., Ewry, E.M., 2020. On a search for a neurogenomics of cognitive processes supporting avian migration and navigation. Integr. Comp. Biol. 60, 967–975.

Bingman, V.P., MacDougall-Shackleton, S.A., 2017. The avian hippocampus and the hypothetical maps used by navigating migratory birds (with some reflection on compasses and migratory restlessness). J. Comp. Physiol. A. 203, 465–474.

Bingman, V.P., Sharp, P.E., 2006. Neuronal implementation of hippocampal-mediated spatial behavior: a comparative evolutionary perspective. Behav. Cogn. Neurosci. Rev. 5, 80–91.

Bingman, V.P., Bagnoli, P., Ioale, P., Casini, G., 1984. Homing behavior of pigeons after telencephalic ablations. Brain Behav. Evol. 24, 94–108.

Bingman, V.P., Gagliardo, A., Hough 2nd, G.E., Ioale, P., Kahn, M.C., Siegel, J.J., 2005. The avian hippocampus, homing in pigeons and the memory representation of large-scale space. Integr. Comp. Biol. 45, 555–564.

Bingman, V.P., Erichsen, J.T., Anderson, J.D., Good, M.A., Pearce, J.M., 2006. Spared feature-structure discrimination but diminished salience of environmental geometry in hippocampal-lesioned homing pigeons (Columba livia). Behav. Neurosci. 120, 835–841.

Bliss, T.V., Lømo, T., 1973. Long-lasting potentiation of synaptic transmission in the dentate area of the anaesthetized rabbit following stimulation of the perforant path. J. Physiol. 232, 331–356.

Bons, N., Bouille, C., Bayle, J.D., Assenmacher, I., 1976. Light and electron microscopic evidence of hypothalamic afferences originating from the hippocampus in the pigeon. Experientia 32, 1443–1445.

Bouillé, C., Baylé, J.D., 1973. Effects of limbic stimulations or lesions on basal and stress-induced hypothalamic-pituitary-adrenocortical activity in the pigeon. Neuroendocrinology 13, 264–277.

Bouille, C., Bayle, J.D., 1976. Comparison between hypothalamic, hippocampal and septal multiple unit activity and basal corticotropic function in unrestrained, unanesthetized resting pigeons. Neuroendocrinology 22, 164–174.

Bouille, C., Bayle, J.D., 1978. Comparison between hypothalamic multiple-unit activity and corticotropic function after bilateral destruction of the hippocampus. Neuroendocrinology 25, 303–309.

BrainMaps: An Interactive Mutiresolution Brain Atlas. Retrieved 28 July 2023 from. http://brainmaps.org.

Broadbent, N., Colombo, M., 2000. Visual and spatial discrimination behavior following hippocampal lesions in pigeons. Psychobiology 28, 463–475.

Brodbeck, D.R., Shettleworth, S.J., 1995. Matching location and color of a compound stimulus - comparison of a food-storing and a nonstoring bird species. J. Exp. Psychol. Anim. B 21, 64–77.

Brown, C.L.J., Zaytsoff, S.J.M., Iwaniuk, A.N., Metz, G.A.S., Montina, T., Inglis, G.D., 2023. Comparative analysis of the temporal impacts of corticosterone and simulated production stressors on the metabolome of broiler chickens. Metabolites 13 (2), 144.

Brown, J.P., Couillard-Despres, S., Cooper-Kuhn, C.M., Winkler, J., Aigner, L., Kuhn, H. G., 2003. Transient expression of doublecortin during adult neurogenesis. J. Comp. Neurol. 467, 1–10.

Bryant, K.G., Barker, J.M., 2020. Arbitration of approach-avoidance conflict by ventral hippocampus. Front. Neurosci. 14, 615337.

Burd, G.D., Nottebohm, F., 1985. Ultrastructural characterization of synaptic terminals formed on newly generated neurons in a song control nucleus of the adult canary forebrain. J. Comp. Neurol. 240, 143–152.

Calhoon, G.G., Tye, K.M., 2015. Resolving the neural circuits of anxiety. Nat. Neurosci. 18, 1394–1404.

Cameron, H.A., Gould, E., 1994. Adult neurogenesis is regulated by adrenal steroids in the dentate gyrus. Neuroscience 61, 203–209.

Carpenter, M.B., Nakano, K., Kim, R., 1976. Nigrothalamic projections in the monkey demonstrated by autoradiographic technics. J. Comp. Neurol. 165, 401–415.

Casini, G., Bingman, V.P., Bagnoli, P., 1986. Connections of the pigeon dorsomedial forebrain studied with WGA-HRP and ^{3}H-proline. J. Comp. Neurol. 245, 454–470.

Chawla, M., Guzowski, J., Ramirez-Amaya, V., Lipa, P., Hoffman, K., Marriott, L., Worley, P., McNaughton, B., Barnes, C.A., 2005. Sparse, environmentally selective expression of Arc RNA in the upper blade of the rodent fascia dentata by brief spatial experience. Hippocampus 15, 579–586.

Clayton, N.S., Krebs, J.R., 1994. Memory for spatial and object-specific cues in food-storing and non-storing birds. J. Comp. Physiol. A. 174, 371–379.

Clayton, N.S., Reboreda, J.C., Kacelnik, A., 1997. Seasonal changes of hippocampus volume in parasitic cowbirds. Behav. Process. 41, 237–243.

Colombo, M., Broadbent, N., 2000. Is the avian hippocampus a functional homologue of the mammalian hippocampus? Neurosci. Biobehav. Rev. 24, 465–484.

Coppola, V.J., Spencer, J.M., Peterson, R.M., Bingman, V.P., 2014. Hippocampal lesions in homing pigeons do not impair feature-quality or feature-quantity discrimination. Behav. Brain Res. 260, 83–91.

Cornelius, J.M., Perreau, G., Bishop, V.R., Krause, J.S., Smith, R., Hahn, T.P., Meddle, S. L., 2018. Social information changes stress hormone receptor expression in the songbird brain. Horm. Behav. 97, 31–38.

Damphousse, C.C., Miller, N., Marrone, D.F., 2022. Functional dissociation along the rostrocaudal axis of Japanese quail hippocampus. PLoS One 17, e0277414.

Danielson, N.B., Kaifosh, P., Zaremba, J.D., Lovett-Barron, M., Tsai, J., Denny, C.A., Balough, E.M., Goldberg, A.R., Drew, L.J., Hen, R., 2016. Distinct contribution of adult-born hippocampal granule cells to context encoding. Neuron 90, 101–112.

Day, L.B., Guerra, M., Schlinger, B.A., Rothstein, S.I., 2008. Sex differences in the effects of captivity on hippocampus size in brown-headed cowbirds (Molothrus ater obscurus). Behav. Neurosci. 122, 527–534.

de Kloet, E.R., 2008. About stress hormones and resilience to psychopathology. J. Neuroendocrinol. 20, 885–892.

de Kloet, E.R., 2014. From receptor balance to rational glucocorticoid therapy. Endocrinology 155, 2754–2769.

Dickens, M., Romero, L.M., Cyr, N.E., Dunn, I.C., Meddle, S.L., 2009. Chronic stress alters glucocorticoid receptor and mineralocorticoid receptor mRNA expression in the European starling (Sturnus vulgaris) brain. J. Neuroendocrinol. 21, 832–840.

Dickens, M.J., Meddle, S.L., Romero, L.M., 2011. Mineralocorticoid and glucocorticoid receptor mRNA expression in the brain of translocated chukar (Alectoris chukar). Gen. Comp. Endocrinol. 170, 569–574.

El-Falougy, H., Benuska, J., 2006. History, anatomical nomenclature, comparative anatomy and functions of the hippocampal formation. Bratisl. Lek. Listy 107, 103–106.

Elliott, B.L., D'Ardenne, K., Murty, V.P., Brewer, G.A., McClure, S.M., 2022. Midbrain-hippocampus structural connectivity selectively predicts motivated memory encoding. J. Neurosci. 42, 9426–9434.

Erichsen, J.T., Bingman, V.P., Krebs, J.R., 1991. The distribution of neuropeptides in the dorsomedial telencephalon of the pigeon (Columba livia): a basis for regional subdivisions. J. Comp. Neurol. 314, 478–492.

Eriksson, P.S., Perfilieva, E., Björk-Eriksson, T., Alborn, A.-M., Nordborg, C., Peterson, D. A., Gage, F.H., 1998. Neurogenesis in the adult human hippocampus. Nat. Med. 4, 1313–1317.

Faber, H., Braun, K., Zuschratter, W., Scheich, H., 1989. System-specific distribution of zinc in the chick brain: a light- and electron-microscopic study using the Timm method. Cell Tissue Res. 258, 247–257.

Fanselow, M.S., Dong, H.W., 2010. Are the dorsal and ventral hippocampus functionally distinct structures? Neuron 65, 7–19.

Farrar, V.S., Morales Gallardo, J., Calisi, R.M., 2022. Prior parental experience attenuates hormonal stress responses and alters hippocampal glucocorticoid receptors in biparental rock doves. J. Exp. Biol. 225.

Felix, B., Roesch, T., 1984. Lateral hypothalamic relations with medial hypothalamus and limbic areas in geese. Brain Res. Bull. 13, 509–517.

Forlano, P.M., Deitcher, D.L., Myers, D.A., Bass, A.H., 2001. Anatomical distribution and cellular basis for high levels of aromatase activity in the brain of teleost fish: aromatase enzyme and mRNA expression identify glia as source. J. Neurosci. 21, 8943–8955.

Fujita, T., Aoki, N., Mori, C., Fujita, E., Matsushima, T., Homma, K.J., Yamaguchi, S., 2022. Chick hippocampal formation displays subdivision- and layer-selective expression patterns of serotonin receptor subfamily genes. Front. Physiol. 13, 882633.

Gagliardo, A., 2013. Forty years of olfactory navigation in birds. J. Exp. Biol. 216, 2165–2171.

Gagliardo, A., Ioale, P., Savini, M., Dell'Omo, G., Bingman, V.P., 2009. Hippocampal-dependent familiar area map supports corrective re-orientation following navigational error during pigeon homing: a GPS-tracking study. Eur. J. Neurosci. 29, 2389–2400.

Gagliardo, A., Pollonara, E., Coppola, V.J., Santos, C.D., Wikelski, M., Bingman, V.P., 2014. Evidence for perceptual neglect of environmental features in hippocampal-lesioned pigeons during homing. Eur. J. Neurosci. 40, 3102–3110.

Gagliardo, A., Pollonara, E., Casini, G., Rossino, M.G., Wikelski, M., Bingman, V.P., 2020. Importance of the hippocampus for the learning of route fidelity in homing pigeons. Biol. Lett. 16, 20200095.

Gagliardo, A., Cioccarelli, S., Giunchi, D., Pollonara, E., Colombo, S., Casini, G., Bingman, V.P., 2023. Deconstructing the flight paths of hippocampal-lesioned homing pigeons as they navigate near home offers insight into spatial perception and memory without a hippocampus. Behav. Brain Res. 436, 114073.

Gahr, M., Güttinger, H.-R., Kroodsma, D.E., 1993. Estrogen receptors in the avian brain: survey reveals general distribution and forebrain areas unique to songbirds. J. Comp. Neurol. 327, 112–122.

Gall, C., 1990. Comparative anatomy of the hippocampus. In: Jones, E.G., Peters, A. (Eds.), Cerebral Cortex. Springer, Boston, MA, pp. 167–213.

Gedman, G., Haase, B., Durieux, G., Biegler, M.T., Fedrigo, O., Jarvis, E.D., 2021. As above, so below: whole transcriptome profiling demonstrates strong molecular similarities between avian dorsal and ventral pallial subdivisions. J. Comp. Neurol. 529, 3222–3246.

Gibbs, M.E., Bowser, D.N., Hutchinson, D.S., Loiacono, R.E., Summers, R.J., 2008. Memory processing in the avian hippocampus involves interactions between β-adrenoceptors, glutamate receptors, and metabolism. Neuropsychopharmacology 33, 2831–2846.

Goldman, S.A., Nottebohm, F., 1983. Neuronal production, migration, and differentiation in a vocal control nucleus of the adult female canary brain. Proc. Natl. Acad. Sci. U. S. A. 80, 2390–2394.

Gould, E., Reeves, A.J., Fallah, M., Tanapat, P., Gross, C.G., Fuchs, E., 1999. Hippocampal neurogenesis in adult old world primates. Proc. Natl. Acad. Sci. 96, 5263–5267.

Gray, J.A., 1977. Drug effects on fear and frustration: possible limbic site of action of minor tranquilizers. Drugs Neurotransmit. Behav. 433–529.

Gray, J.A., 1982. Précis of the neuropsychology of anxiety: an enquiry into the functions of the septo-hippocampal system. Behav. Brain Sci. 5, 469–484.

Gray, J.A., 1987. Perspectives on anxiety and impulsivity - a commentary. J. Res. Pers. 21, 493–509.

Gray, J.A., McNaughton, N., 2000. The Neuropsychology of Anxiety. Oxford University Press, Oxford, An Enquiry into the Functions of the Septo-Hippocampal System.

Greenberg, R., 1990. Feeding Neophobia and ecological plasticity - a test of the hypothesis with captive sparrows. Anim. Behav. 39, 375–379.

Gualtieri, F., Armstrong, E.A., Longmoor, G.K., D'Eath, R.B., Sandilands, V., Boswell, T., Smulders, T.V., 2019. Unpredictable chronic mild stress suppresses the incorporation of new neurons at the caudal pole of the chicken hippocampal formation. Sci. Rep. 9, 7129.

Gupta, S., Maurya, R., Saxena, M., Sen, J., 2012. Defining structural homology between the mammalian and avian hippocampus through conserved gene expression patterns observed in the chick embryo. Dev. Biol. 366, 125–141.

Hampton, R.R., Shettleworth, S.J., 1996. Hippocampus and memory in a food-storing and in a nonstoring bird species. Behav. Neurosci. 110, 946–964.

Hawley, D.F., Leasure, J.L., 2012. Region-specific response of the hippocampus to chronic unpredictable stress. Hippocampus 22, 1338–1349.

Healy, S., Krebs, J., Gwinner, E., 1991. Hippocampal volume and migration in passerine birds. Sci. Nat. 78, 424–426.

Healy, S., Gwinner, E., Krebs, J., 1996. Hippocampal volume in migratory and non-migratory warblers: effects of age and experience. Behav. Brain Res. 81, 61–68.

Herold, C., Bingman, V.P., Strockens, F., Letzner, S., Sauvage, M., Palomero-Gallagher, N., Zilles, K., Gunturkun, O., 2014. Distribution of neurotransmitter receptors and zinc in the pigeon (*Columba livia*) hippocampal formation: a basis for further comparison with the mammalian hippocampus. J. Comp. Neurol. 522, 2553–2575.

Herold, C., Coppola, V.J., Bingman, V.P., 2015. The maturation of research into the avian hippocampal formation: recent discoveries from one of the nature's foremost navigators. Hippocampus 25, 1193–1211.

Herold, C., Schlomer, P., Mafoppa-Fomat, I., Mehlhorn, J., Amunts, K., Axer, M., 2019. The hippocampus of birds in a view of evolutionary connectomics. Cortex 118, 165–187.

Heyers, D., Musielak, I., Haase, K., Herold, C., Bolte, P., Güntürkün, O., Mouritsen, H., 2022. Morphology, biochemistry and connectivity of cluster N and the hippocampal formation in a migratory bird. Brain Struct. Funct. 227, 2731–2749.

Hodgson, Z.G., Meddle, S.L., Roberts, M.L., Buchanan, K.L., Evans, M.R., Metzdorf, R., Gahr, M., Healy, S.D., 2007. Spatial ability is impaired and hippocampal mineralocorticoid receptor mRNA expression reduced in zebra finches (*Taeniopygia guttata*) selected for acute high corticosterone response to stress. Proc. R. Soc. B Biol. Sci. 274, 239–245.

Hodgson, Z.G., Meddle, S.L., Christians, J.K., Sperry, T.S., Healy, S.D., 2008. Influence of sex steroid hormones on spatial memory in a songbird. J. Comp. Physiol. A. 194, 963–969.

Hough, G.E., Bingman, V.P., 2004. Spatial response properties of homing pigeon hippocampal neurons: correlations with goal locations, movement between goals, and environmental context in a radial-arm arena. J. Comp. Physiol. A. 190, 1047–1062.

Hough, G.E., Pang, K.C.H., Bingman, V.P., 2002. Intrahippocampal connections in the pigeon (*Columba livia*) as revealed by stimulation evoked field potentials. J. Comp. Neurol. 452, 297–309.

Ito, R., Lee, A.C.H., 2016. The role of the hippocampus in approach-avoidance conflict decision-making: evidence from rodent and human studies. Behav. Brain Res. 313, 345–357.

Jacobson, L., Sapolsky, R.M., 1991. The role of the hippocampus in feedback regulation of the hypothalamic-pituitary-adrenocortical axis. Endocr. Rev. 12, 118–134.

Jarvis, E.D., Yu, J., Rivas, M.V., Horita, H., Feenders, G., Whitney, O., Jarvis, S.C., Jarvis, E.R., Kubikova, L., Puck, A.E., Siang-Bakshi, C., Martin, S., McElroy, M., Hara, E., Howard, J., Pfenning, A., Mouritsen, H., Chen, C.C., Wada, K., 2013. Global view of the functional molecular organization of the avian cerebrum: mirror images and functional columns. J. Comp. Neurol. 521, 3614–3665.

Jayatissa, M.N., Bisgaard, C., Tingström, A., Papp, M., Wiborg, O., 2006. Hippocampal cytogenesis correlates to escitalopram-mediated recovery in a chronic mild stress rat model of depression. Neuropsychopharmacology 31, 2395–2404.

Jeong, Y., Huh, N., Lee, J., Yun, I., Lee, J.W., Lee, I., Jung, M.W., 2018. Role of the hippocampal CA1 region in incremental value learning. Sci. Rep. 8, 9870.

Jin, S.W., Lee, I., 2021. Differential encoding of place value between the dorsal and intermediate hippocampus. Curr. Biol. 31, 3053–3072.

Joels, M., de Kloet, E.R., 1994. Mineralocorticoid and glucocorticoid receptors in the brain. Implications for ion permeability and transmitter systems. Prog. Neurobiol. 43, 1–36.

Joels, M., Karst, H., DeRijk, R., de Kloet, E.R., 2008. The coming out of the brain mineralocorticoid receptor. Trends Neurosci. 31, 1–7.

Johnston, M., Scarf, D., Wilson, A., Millar, J., Bartonicek, A., Colombo, M., 2020. The effects of hippocampal and area parahippocampalis lesions on the processing and retention of serial-order behavior, autoshaping, and spatial behavior in pigeons. Hippocampus 31, 261–280.

Jung, M.W., McNaughton, B.L., 1993. Spatial selectivity of unit activity in the hippocampal granular layer. Hippocampus 3, 165–182.

Jung, M.W., Lee, H., Jeong, Y., Lee, J.W., Lee, I., 2018. Remembering rewarding futures: a simulation-selection model of the hippocampus. Hippocampus 28, 913–930.

Kahn, M.C., Bingman, V.P., 2009. Avian hippocampal role in space and content memory. Eur. J. Neurosci. 30, 1900–1908.

Kahn, M.C., Hough 2nd, G.E., Ten Eyck, G.R., Bingman, V.P., 2003. Internal connectivity of the homing pigeon (Columba livia) hippocampal formation: an anterograde and retrograde tracer study. J. Comp. Neurol. 459, 127–141.

Kahn, M.C., Siegel, J.J., Jechura, T.J., Bingman, V.P., 2008. Response properties of avian hippocampal formation cells in an environment with unstable goal locations. Behav. Brain Res. 191, 153–163.

Kaplan, M.S., Hinds, J.W., 1977. Neurogenesis in the adult rat: electron microscopic analysis of light radioautographs. Science 197, 1092–1094.

Karten, H., Hodos, W., 1967. A Stereotaxic Atlas of the Brain of the Pigeon: *Columba Livia*.

Kimball, M.G., Gautreaux, E.B., Couvillion, K.E., Kelly, T.R., Stansberry, K.R., Lattin, C.R., 2022. Novel objects alter immediate early gene expression globally for ZENK and regionally for c-Fos in neophobic and non-neophobic house sparrows. Behav. Brain Res. 428, 113863.

Knierim, J.J., 2015. The hippocampus. Curr. Biol. 25, R1116–R1121.

Korte, S.M., Koolhaas, J.M., Wingfield, J.C., McEwen, B.S., 2005. The Darwinian concept of stress: benefits of allostasis and costs of allostatic load and the trade-offs in health and disease. Neurosci. Biobehav. Rev. 29, 3–38.

Krause, J.S., McGuigan, M.A., Bishop, V.R., Wingfield, J.C., Meddle, S.L., 2015. Decreases in mineralocorticoid but not glucocorticoid receptor mRNA expression during the short Arctic breeding season in free-living Gambel's white-crowned sparrow (Zonotrichia leucophrys gambelii). J. Neuroendocrinol. 27, 66–75.

Krause, J.S., Pérez, J.H., Chmura, H.E., Meddle, S.L., Hunt, K.E., Gough, L., Boelman, N., Wingfield, J.C., 2016. The stress response is attenuated during inclement weather in parental, but not in pre-parental, Lapland longspurs (*Calcarius lapponicus*) breeding in the low Arctic. Horm. Behav. 83, 68–74.

Krause, J.S., Perez, J.H., Meddle, S.L., Wingfield, J.C., 2017. Effects of short-term fasting on stress physiology, body condition, and locomotor activity in wintering male white-crowned sparrows. Physiol. Behav. 177, 282–290.

Krause, J.S., Perez, J.H., Reid, A.M.A., Cheah, J., Bishop, V., Wingfield, J.C., Meddle, S.L., 2021. Acute restraint stress does not alter corticosteroid receptors or 11beta-hydroxysteroid dehydrogenase gene expression at hypothalamic-pituitary-adrenal axis regulatory sites in captive male white-crowned sparrows (*Zonotrichia leucophrys gambelii*). Gen. Comp. Endocrinol. 303, 113701.

Krebs, J.R., Sherry, D.F., Healy, S.D., Perry, V.H., Vaccarino, A.L., 1989. Hippocampal specialization of food-storing birds. Proc. Natl. Acad. Sci. 86, 1388–1392.

Krebs, J.R., Erichsen, J.T., Bingman, V.P., 1991. The distribution of neurotransmitters and neurotransmitter-related enzymes in the dorsomedial telencephalon of the pigeon (Columba livia). J. Comp. Neurol. 314, 467–477.

Krishnan, S., Heer, C., Cherian, C., Sheffield, M.E.J., 2022. Reward expectation extinction restructures and degrades CA1 spatial maps through loss of a dopaminergic reward proximity signal. Nat. Commun. 13, 6662.

Krohmer, R.W., Bieganski, G.J., Baleckaitis, D.D., Harada, N., Balthazart, J., 2002. Distribution of aromatase immunoreactivity in the forebrain of red-sided garter snakes at the beginning of the winter dormancy. J. Chem. Neuroanat. 23, 59–71.

Krushinskaya, N., 1966. Some complex forms of feeding behaviour of nutcracker Nucifraga caryocatactes, after removal of old cortex. Zh Evol Biokhim Fisiol 11, 563–568.

Kumar, A., Tamta, K., Arya, H., Maurya, R.C., 2023. Acute-stress induces the structural plasticity in hippocampal neurons of 15 and 30-day-old chick, Gallus domesticus. Ann. Anat. 245, 151996.

LaDage, L.D., Roth, T.C., Fox, R.A., Pravosudov, V.V., 2009. Effects of captivity and memory-based experiences on the hippocampus in mountain chickadees. Behav. Neurosci. 123, 284–291.

LaDage, L.D., Roth 2nd, T.C., Fox, R.A., Pravosudov, V.V., 2010. Ecologically relevant spatial memory use modulates hippocampal neurogenesis. Proc. R. Soc. B 277, 1071–1079.

Landys, M.M., Piersma, T., Ramenofsky, M., Wingfield, J.C., 2004. Role of the low-affinity glucocorticoid receptor in the regulation of behavior and energy metabolism in the migratory red knot Calidris canutus islandica. Physiol. Biochem. Zool. 77, 658–668.

Lange, H., Walker, L., Orell, M., Smulders, T.V., 2022. Seasonal changes in the hippocampal formation of hoarding and non-hoarding tits. Learn. Behav. 50, 113–124.

Larosa, A., Wong, T.P., 2022. The hippocampus in stress susceptibility and resilience: reviewing molecular and functional markers. Prog. Neuro-Psychopharmacol. Biol. Psychiatry 119, 110601.

Lattin, C.R., Romero, L.M., 2013. Seasonal variation in corticosterone receptor binding in brain, hippocampus, and gonads in house sparrows (Passer Domesticus). Auk 130, 591–598.

Lattin, C.R., Waldron-Francis, K., Richardson, J.W., de Bruijn, R., Bauer, C.M., Breuner, C.W., Michael Romero, L., 2012. Pharmacological characterization of intracellular glucocorticoid receptors in nine tissues from house sparrow (*Passer domesticus*). Gen. Comp. Endocrinol. 179, 214–220.

Lattin, C.R., Kelly, T.R., Kelly, M.W., Johnson, K.M., 2022. Constitutive gene expression differs in three brain regions important for cognition in neophobic and non-neophobic house sparrows (Passer domesticus). PLoS One 17, e0267180.

Lee-Teng, E., Sherman, S.M., 1966. Memory consolidation of one-trial learning in chicks. Proc. Natl. Acad. Sci. U. S. A. 56, 926–931.

Lemaire, V., Aurousseau, C., Le Moal, M., Abrous, D.N., 1999. Behavioural trait of reactivity to novelty is related to hippocampal neurogenesis. Eur. J. Neurosci. 11, 4006–4014.

Loh, E., Kurth-Nelson, Z., Berron, D., Dayan, P., Duzel, E., Dolan, R., Guitart-Masip, M., 2017. Parsing the role of the hippocampus in approach-avoidance conflict. Cereb. Cortex 27, 201–215.

Lörincz, A., Buzsáki, G., 2000. Two-phase computational model training long-term memories in the entorhinal-hippocampal region. Ann. N. Y. Acad. Sci. 911, 83–111.

Lormant, F., Ferreira, V.H.B., Meurisse, M., Lemarchand, J., Constantin, P., Morisse, M., Cornilleau, F., Parias, C., Chaillou, E., Bertin, A., Lansade, L., Leterrier, C., Levy, F.,

Calandreau, L., 2020. Emotionality modulates the impact of chronic stress on memory and neurogenesis in birds. Sci. Rep. 10, 14620.

Lotvedt, P., Fallahshahroudi, A., Bektic, L., Altimiras, J., Jensen, P., 2017. Chicken domestication changes expression of stress-related genes in brain, pituitary and adrenals. Neurobiol. Stress 7, 113–121.

Mayer, U., Bischof, H.J., 2012. Brain activation pattern depends on the strategy chosen by zebra finches to solve an orientation task. J. Exp. Biol. 215, 426–434.

Mayer, U., Watanabe, S., Bischof, H.J., 2010. Hippocampal activation of immediate early genes Zenk and c-Fos in zebra finches (*Taeniopygia guttata*) during learning and recall of a spatial memory task. Neurobiol. Learn. Mem. 93, 322–329.

McNaughton, N., Gray, J.A., 2000. Anxiolytic action on the behavioural inhibition system implies multiple types of arousal contribute to anxiety. J. Affect. Disord. 61, 161–176.

Mehlhorn, J., Niski, N., Liu, K., Caspers, S., Amunts, K., Herold, C., 2022. Regional patterning of adult neurogenesis in the homing pigeon's brain. Front. Psychol. 13, 889001.

Mello, C.V., Kaser, T., Buckner, A.A., Wirthlin, M., Lovell, P.V., 2019. Molecular architecture of the zebra finch arcopallium. J. Comp. Neurol. 527, 2512–2556.

Metzdorf, R., Gahr, M., Fusani, L., 1999. Distribution of aromatase, estrogen receptor, and androgen receptor mRNA in the forebrain of songbirds and nonsongbirds. J. Comp. Neurol. 407, 115–129.

Mills, A.D., Faure, J.M., 1991. Divergent selection for duration of tonic immobility and social reinstatement behavior in Japanese quail (*Coturnix coturnix japonica*) chicks. J. Comp. Psychol. 105, 25–38.

Mizumori, S.J., Tryon, V.L., 2015. Integrative hippocampal and decision-making neurocircuitry during goal-relevant predictions and encoding. Prog. Brain Res. 219, 217–242.

Moaraf, S., Heiblum, R., Vistoropsky, Y., Okuliarova, M., Zeman, M., Barnea, A., 2020a. Artificial light at night increases recruitment of new neurons and differentially affects various brain regions in female zebra finches. Int. J. Mol. Sci. 21, 6140.

Moaraf, S., Vistoropsky, Y., Pozner, T., Heiblum, R., Okuliarova, M., Zeman, M., Barnea, A., 2020b. Artificial light at night affects brain plasticity and melatonin in birds. Neurosci. Lett. 716, 134639.

Moaraf, S., Heiblum, R., Okuliarova, M., Hefetz, A., Scharf, I., Zeman, M., Barnea, A., 2021. Evidence that artificial light at night induces structure-specific changes in brain plasticity in a diurnal bird. Biomolecules 11.

Montagnese, C.M., Krebs, J.R., Székely, A.D., Csillag, A., 1993. A subpopulation of large calbindin-like immunopositive neurones is present in the hippocampal formation in food-storing but not in non-storing species of bird. Brain Res. 614, 291–300.

Montagnese, C.M., Krebs, J.R., Meyer, G., 1996. The dorsomedial and dorsolateral forebrain of the zebra finch, *Taeniopygia guttata*: a Golgi study. Cell Tissue Res. 283, 263–282.

Morandi-Raikova, A., Mayer, U., 2021. Selective activation of the right hippocampus during navigation by spatial cues in domestic chicks (*Gallus gallus*). Neurobiol. Learn. Mem. 177, 107344.

Morris, R.G., 2003. Long-term potentiation and memory. Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci. 358, 643–647.

Morris, R.G., Garrud, P., Rawlins, J.N., O'Keefe, J., 1982. Place navigation impaired in rats with hippocampal lesions. Nature 297, 681–683.

Nau, M., Julian, J.B., Doeller, C.F., 2018. How the brain's navigation system shapes our visual experience. Trends Cogn. Sci. 22, 810–825.

Nikolakopoulou, A.M., 2005. Neural and Synaptic Plasticity in the Chick Brain After Passive Avoidance Learning. The Open University, p. 235.

Nikolakopoulou, A.M., Davies, H.A., Stewart, M.G., 2006a. Passive avoidance training decreases synapse density in the hippocampus of the domestic chick. Eur. J. Neurosci. 23, 1054–1062.

Nikolakopoulou, A.M., Dermon, C.R., Panagis, L., Pavlidis, M., Stewart, M.G., 2006b. Passive avoidance training is correlated with decreased cell proliferation in the chick hippocampus. Eur. J. Neurosci. 24, 2631–2642.

O'Connell, L.A., Hofmann, H.A., 2011. The vertebrate mesolimbic reward system and social behavior network: a comparative synthesis. J. Comp. Neurol. 519, 3599–3639.

O'Keefe, J., Dostrovsky, J., 1971. The hippocampus as a spatial map: preliminary evidence from unit activity in the freely-moving rat. Brain Res. 34, 171–175.

O'Keefe, J., Nadel, L., 1978. The Hippocampus as a Cognitive Map. Oxford Univ. Press, Oxford.

O'Leary, O.F., Cryan, J.F., 2014. A ventral view on antidepressant action: roles for adult hippocampal neurogenesis along the dorsoventral axis. Trends Pharmacol. Sci. 35, 675–687.

O'Neil, E.B., Newsome, R.N., Li, I.H., Thavabalasingam, S., Ito, R., Lee, A.C., 2015. Examining the role of the human hippocampus in approach-avoidance decision making using a novel conflict paradigm and multivariate functional magnetic resonance imaging. J. Neurosci. 35, 15039–15049.

Ortiz, J.B., Conrad, C.D., 2018. The impact from the aftermath of chronic stress on hippocampal structure and function: is there a recovery? Front. Neuroendocrinol. 49, 114–123.

Paton, J.A., Nottebohm, F.N., 1984. Neurons generated in the adult brain are recruited into functional circuits. Science 225, 1046–1048.

Payne, H.L., Lynch, G.F., Aronov, D., 2021. Neural representations of space in the hippocampus of a food-caching bird. Science 373, 343–348.

Pentkowski, N.S., Blanchard, D.C., Lever, C., Litvin, Y., Blanchard, R.J., 2006. Effects of lesions to the dorsal and ventral hippocampus on defensive behaviors in rats. Eur. J. Neurosci. 23, 2185–2196.

Peterson, R.S., Yarram, L., Schlinger, B.A., Saldanha, C.J., 2005. Aromatase is presynaptic and sexually dimorphic in the adult zebra finch brain. Proc. Biol. Sci. 272, 2089–2096.

Phillmore, L.S., Aitken, S.D.T., Parks, B.M.B., 2022. Understanding hippocampal neural plasticity in captivity: unique contributions of spatial specialists. Learn. Behav. 50, 55–70.

Plachti, A., Eickhoff, S.B., Hoffstaedter, F., Patil, K.R., Laird, A.R., Fox, P.T., Amunts, K., Genon, S., 2019. Multimodal parcellations and extensive behavioral profiling tackling the hippocampus gradient. Cereb. Cortex 29, 4595–4612.

Pravosudov, V.V., 2022. Do Food-caching Chickadees Grow Their Hippocampus Every Autumn When They Need to Cache Food and Then Shrink It for the Rest of the Year? Animal Behaviour 190.

Pravosudov, V.V., Clayton, N.S., 2002. A test of the adaptive specialization hypothesis: population differences in caching, memory, and the hippocampus in black-capped chickadees (*Poecile atricapilla*). Behav. Neurosci. 116, 515–522.

Pravosudov, V.V., Omanska, A., 2005. Dominance-related changes in spatial memory are associated with changes in hippocampal cell proliferation rates in mountain chickadees. J. Neurobiol. 62, 31–41.

Pravosudov, V.V., Roth, T.C., 2013. Cognitive ecology of food hoarding: the evolution of spatial memory and the hippocampus. Annu. Rev. Ecol. Evol. Syst. 44, 173–193.

Pravosudov, V.V., Kitaysky, A.S., Omanska, A., 2006. The relationship between migratory behaviour, memory and the hippocampus: an intraspecific comparison. Proc. R. Soc. B Biol. Sci. 273, 2641–2649.

Puelles, L., Martinez-de-la-Torre, M., Martinez, S., Watson, C., Paxinos, G., 2007. The Chick Brain in Stereotaxic Coordinates: An Atlas Featuring Neuromeric Subdivisions and Mammalian Homologies. Academic Press, Cambridge, MA.

Ramade, F., Nouguier, J., Baylé, J.D., 1979. Etude cinétique de la réponse corticosurrénalienne à la télestimulation de l'hypothalamus du pigeon thalamique. C. R. Seances Soc. Biol. 173, 1109–1112.

Rao, M.S., Shetty, A.K., 2004. Efficacy of doublecortin as a marker to analyse the absolute number anddendritic growth of newly generated neurons in the adult dentate gyrus. Eur. J. Neurosci. 19, 234–246.

Reboreda, J.C., Clayton, N.S., Kacelnik, A., 1996. Species and sex differences in hippocampus size in parasitic and non-parasitic cowbirds. NeuroReport 7, 505–508.

Rehkämper, G., Haase, E., Frahm, H.D., 1988. Allometric comparison of brain weight and brain structure volumes in different breeds of the domestic pigeon, *Columba livia* f.d. (fantails, homing pigeons, strassers). Brain Behav. Evol. 31, 141–149.

Rickels, K., 1978. Use of antianxiety agents in anxious outpatients. Psychopharmacology 58, 1–17.

Robertson, B.-A., Rathbone, L., Cirillo, G., D'Eath, R.B., Bateson, M., Boswell, T., Wilson, P.W., Dunn, I.C., Smulders, T.V., 2017. Food restriction reduces neurogenesis in the avian hippocampal formation. PLoS One 12, e0189158.

Romero, L.M., 2004. Physiological stress in ecology: lessons from biomedical research. Trends Ecol. Evol. 19, 249–255.

Rook, N., Stacho, M., Schwarz, A., Bingman, V.P., Gunturkun, O., 2023. Neuronal Circuits Within the Homing Pigeon Hippocampal Formation. J Comp Neurol.

Roth 2nd, T.C., Stocker, K., Mauck, R., 2017. Morphological changes in hippocampal cytoarchitecture as a function of spatial treatment in birds. Dev. Neurobiol. 77, 93–101.

Roth, T.C., la Dage, L.D., Freas, C.A., Pravosudov, V.V., 2012. Variation in memory and the hippocampus across populations from different climates: a common garden approach. Proc. R. Soc. B 279, 402–410.

Russell, J.A., 1980. A circumplex model of affect. J. Pers. Soc. Psychol. 39, 1161–1178.

Saldanha, C.J., Popper, P., Micevych, P.E., Schlinger, B.A., 1998. The passerine hippocampus is a site of high aromatase: inter- and intraspecies comparisons. Horm. Behav. 34, 85–97.

Salwiczek, L.H., Watanabe, A., Clayton, N.S., 2010. Ten years of research into avian models of episodic-like memory and its implications for developmental and comparative cognition. Behav. Brain Res. 215, 221–234.

Sandi, C., Rose, S.P., 1997. Training-dependent biphasic effects of corticosterone in memory formation for a passive avoidance task in chicks. Psychopharmacology 133, 152–160.

Scarf, D., Millar, J., Pow, N., Colombo, M., 2014. Inhibition, the final frontier: the impact of hippocampal lesions on behavioral inhibition and spatial processing in pigeons. Behav. Neurosci. 128, 42–47.

Schaffer, A., Caicoya, A.L., Colell, M., Holland, R., von Fersen, L., Widdig, A., Amici, F., 2021. Neophobia in 10 ungulate species-a comparative approach. Behav. Ecol. Sociobiol. 75, 102.

Senft, R.A., Meddle, S.L., Baugh, A.T., 2016. Distribution and abundance of glucocorticoid and mineralocorticoid receptors throughout the brain of the great tit (*Parus major*). PLoS One 11, e0148516.

Shahbazi, M., Schmidt, M., Carruth, L.L., 2011. Distribution and subcellular localization of glucocorticoid receptor-immunoreactive neurons in the developing and adult male zebra finch brain. Gen. Comp. Endocrinol. 174, 354–361.

Sherry, D.F., Hoshooley, J.S., 2010. Seasonal hippocampal plasticity in food-storing birds. Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci. 365, 933–943.

Sherry, D.F., MacDougall-Shackleton, S.A., 2015. Seasonal change in the avian hippocampus. Front. Neuroendocrinol. 37, 158–167.

Sherry, D.F., Vaccarino, A.L., 1989. Hippocampus and memory for food caches in black-capped chickadees. Behav. Neurosci. 103, 308–318.

Sherry, D.F., Vaccarino, A.L., Buckenham, K., Herz, R.S., 1989. The hippocampal complex of food-storing birds. Brain Behav. Evol. 34, 308–317.

Sherry, D.F., Forbes, M., Khurgel, M., Ivy, G.O., 1993. Females have a larger hippocampus than males in the brood-parasitic brown-headed cowbird. Proc. Natl. Acad. Sci. 90, 7839–7843.

Siegel, J.J., Nitz, D., Bingman, V.P., 2005. Spatial-specificity of single-units in the hippocampal formation of freely moving homing pigeons. Hippocampus 15, 26–40.

Siegel, J.J., Nitz, D., Bingman, V.P., 2006. Lateralized functional components of spatial cognition in the avian hippocampal formation: evidence from single-unit recordings in freely moving homing pigeons. Hippocampus 16, 125–140.

Sizemore, B.A., Bausher, A., Paul, E., Russell, M., Bingman, V.P., 2022. Space, feature, and risk sensitivity in homing pigeons (*Columba livia*): broadening the conversation on the role of the avian hippocampus in memory. Learn. Behav. 50, 99–112.

Smulders, T.V., 2006. A multi-disciplinary approach to understanding hippocampal function in food-hoarding birds. Rev. Neurosci. 17, 53–69.

Smulders, T.V., 2017. The avian hippocampal formation and the stress response. Brain Behav. Evol. 90, 81–91.

Smulders, T.V., 2021. Telencephalic regulation of the HPA axis in birds. Neurobiol. Stress 15, 100351.

Smulders, T.V., Sasson, A.D., DeVoogd, T.J., 1995. Seasonal variation in hippocampal volume in a food-storing bird, the black-capped chickadee. J. Neurobiol. 27, 15–25.

Smulders, T.V., Casto, J.M., Nolan Jr., V., Ketterson, E.D., DeVoogd, T.J., 2000a. Effects of captivity and testosterone on the volumes of four brain regions in the dark-eyed junco (Junco hyemalis). J. Neurobiol. 43, 244–253.

Smulders, T.V., Shiflett, M.W., Sperling, A.J., DeVoogd, T.J., 2000b. Seasonal changes in neuron numbers in the hippocampal formation of a food-hoarding bird: the black-capped chickadee. J. Neurobiol. 44, 414–422.

Sosa, M., Giocomo, L.M., 2021. Navigating for reward. Nat. Rev. Neurosci. 22, 472–487.

Stacho, M., Herold, C., Rook, N., Wagner, H., Axer, M., Amunts, K., Güntürkün, O., 2020. A cortex-like canonical circuit in the avian forebrain. Science 369, eabc5534.

Striedter, G.F., 2016. Evolution of the hippocampus in reptiles and birds. J. Comp. Neurol. 524, 496–517.

Suarez, J., Davila, J.C., Real, M.A., Guirado, S., Medina, L., 2006. Calcium-binding proteins, neuronal nitric oxide synthase, and GABA help to distinguish different pallial areas in the developing and adult chicken. I. Hippocampal formation and hyperpallium. J. Comp. Neurol. 497, 751–771.

Suzuki, K., Matsunaga, E., Kobayashi, T., Okanoya, K., 2011. Expression patterns of mineralocorticoid and glucocorticoid receptors in Bengalese finch (Lonchura striata var. domestica) brain suggest a relationship between stress hormones and song-system development. Neuroscience 194, 72–83.

Székely, A.D., 1999. The avian hippocampal formation: subdivisions and connectivity. Behav. Brain Res. 98, 219–225.

Szekely, A.D., Krebs, J.R., 1996. Efferent connectivity of the hippocampal formation of the zebra finch (*Taenopygia guttata*): an anterograde pathway tracing study using Phaseolus vulgaris leucoagglutinin. J. Comp. Neurol. 368, 198–214.

Takahashi, S., Hombe, T., Matsumoto, S., Ide, K., Yoda, K., 2022. Head direction cells in a migratory bird prefer north. Sci. Adv. 8, eabl6848.

Takeuchi, H., Yazaki, Y., Matsushima, T., Aoki, K., 1996. Expression of Fos-like immunoreactivity in the brain of quail chick emitting the isolation-induced distress calls. Neurosci. Lett. 220, 191–194.

Tarr, B.A., Rabinowitz, J.S., Ali Imtiaz, M., DeVoogd, T.J., 2009. Captivity reduces hippocampal volume but not survival of new cells in a food-storing bird. Dev. Neurobiol. 69, 972–981.

Taufique, S.K.T., Prabhat, A., Kumar, V., 2018a. Constant light environment suppresses maturation and reduces complexity of new born neuron processes in the hippocampus and caudal nidopallium of a diurnal corvid: implication for impairment of the learning and cognitive performance. Neurobiol. Learn. Mem. 147, 120–127.

Taufique, S.K.T., Prabhat, A., Kumar, V., 2018b. Illuminated night alters hippocampal gene expressions and induces depressive-like responses in diurnal corvids. Eur. J. Neurosci. 48, 3005–3018.

Taufique, S.T., Prabhat, A., Kumar, V., 2019. Light at night affects hippocampal and nidopallial cytoarchitecture: implication for impairment of brain function in diurnal corvids. J. Exp. Zool. A Ecol. Integr. Physiol. 331, 149–156.

Tobler, M., Sandell, M.I., 2007. Yolk testosterone modulates persistence of neophobic responses in adult zebra finches, *Taeniopygia guttata*. Horm. Behav. 52, 640–645.

Tommasi, L., Gagliardo, A., Andrew, R.J., Vallortigara, G., 2003. Separate processing mechanisms for encoding of geometric and landmark information in the avian hippocampus. Eur. J. Neurosci. 17, 1695–1702.

Treves, A., Tashiro, A., Witter, M.E., Moser, E.I., 2008. What is the mammalian dentate gyrus good for? Neuroscience 154, 1155–1172.

Ulrich-Lai, Y.M., Herman, J.P., 2009. Neural regulation of endocrine and autonomic stress responses. Nat. Rev. Neurosci. 10, 397–409.

Unal, B., Bradley, P.M., Sahin, B., Canan, S., Aslan, H., Kaplan, S., 2002. Estimation of numerical density and mean synaptic height in chick hippocampus 24 and 48 hours after passive avoidance training. Brain Res. Dev. Brain Res. 136, 135–144.

Vahaba, D.M., Remage-Healey, L., 2015. Brain estrogen production and the encoding of recent experience. Curr. Opin. Behav. Sci. 6, 148–153.

Vanni-Mercier, G., Mauguiere, F., Isnard, J., Dreher, J.C., 2009. The hippocampus codes the uncertainty of cue-outcome associations: an intracranial electrophysiological study in humans. J. Neurosci. 29, 5287–5294.

Vargas, J.P., Petruso, E.J., Bingman, V.P., 2004. Hippocampal formation is required for geometric navigation in pigeons. Eur. J. Neurosci. 20, 1937–1944.

Vellema, M., Hertel, M., Urbanus, S.L., Van der Linden, A., Gahr, M., 2014a. Evaluating the predictive value of doublecortin as a marker for adult neurogenesis in canaries (*Serinus canaria*). J. Comp. Neurol. 522, 1299–1315.

Vellema, M., Ko, M.C., Frankl-Vilches, C., Gahr, M., 2014b. What Makes a Marker a Good Marker?. Commentary on Balthazart J and Ball G (2014): Doublecortin is a highly valuable endogenous marker of adult neurogenesis in canaries. Brain Behav. Evol. 84, 1–4 (Brain, Behavior and Evolution).

Wallraff, H.G., Wallraff, H.G. (Eds.), 2005. Avian Navigation: Pigeon Homing as a Paradigm. Springer Science & Business Media.

White, A.R., Strasser, R., Bingman, V.P., 2002. Hippocampus lesions impair landmark array spatial learning in homing pigeons: a laboratory study. Neurobiol. Learn. Mem. 78, 65–78.

Wiltschko, R., Wiltschko, W., 2003. Avian navigation: from historical to modern concepts. Anim. Behav. 65, 257–272.

Witter, M.P., 2018. Connectivity of the Hippocampus. In: Cutsuridis, V., Graham, B.P., Cobb, S., Vida, I. (Eds.), Hippocampal Microcircuits: A Computational Modeler's Resource Book. Springer International Publishing, Cham, pp. 5–28.

Witter, M.P., Kleven, H., Kobro Flatmoen, A., 2017. Comparative contemplations on the hippocampus. Brain Behav. Evol. 90, 15–24.

Yague, J.G., Wang, A.C., Janssen, W.G., Hof, P.R., Garcia-Segura, L.M., Azcoitia, I., Morrison, J.H., 2008. Aromatase distribution in the monkey temporal neocortex and hippocampus. Brain Res. 1209, 115–127.

Zeidman, P., Mullally, S.L., Maguire, E.A., 2015. Constructing, perceiving, and maintaining scenes: hippocampal activity and connectivity. Cereb. Cortex 25, 3836–3855.

Zimmer, C., Spencer, K.A., 2014. Modifications of glucocorticoid receptors mRNA expression in the hypothalamic-pituitary-adrenal axis in response to early-life stress in female Japanese quail. J. Neuroendocrinol. 26, 853–860.

Zimmer, C., Taff, C.C., Ardia, D.R., Rosvall, K.A., Kallenberg, C., Bentz, A.B., Taylor, A.R., Johnson, L.S., Vitousek, M.N., 2023. Gene expression in the female tree swallow brain is associated with inter- and intra-population variation in glucocorticoid levels. Horm. Behav. 147, 105280.