

Review

Seasonal change in the avian hippocampus



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ABSTRACT

The hippocampus plays an important role in cognitive processes, including memory and spatial orientation, in birds. The hippocampus undergoes seasonal change in food-storing birds and brood parasites, there are changes in the hippocampus during breeding, and further changes occur in some species in association with migration. In food-storing birds, seasonal change in the hippocampus occurs in fall and winter when the cognitively demanding behaviour of caching and retrieving food occurs. The timing of annual change in the hippocampus of food-storing birds is quite variable, however, and appears not to be under photoperiod control. A variety of factors, including cognitive performance, exercise, and stress may all influence seasonal change in the avian hippocampus. The causal processes underlying seasonal change in the avian hippocampus have not been extensively examined and the more fully described hormonal influences on the mammalian hippocampus may provide hypotheses for investigating the control of hippocampal seasonality in birds.

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1. Introduction

1.1. Introduction and scope

The lives of birds are driven by seasonal factors and dramatic changes in behaviour and physiology occur on an annual cycle in many species. Seasonal reproduction is associated with changes in song, courtship, parental care, and plumage of most species (Dawson et al., 2001; Rani and Kumar, 2013). Migration and the physiological changes associated with migration occur just before and again following reproduction in many temperate zone birds (Cornelius et al., 2013). For non-migrants, there are physiological and behavioural changes associated with remaining resident at high latitudes during winter (Witter and Cuthill, 1993; Wingfield and Ramenofsky, 2011). It should not be a surprise, then, that changes also occur in birds' brains on a seasonal time scale. Despite a long history of research on seasonal change in the song-control system and hypothalamic–pituitary–gonadal axis, examination of seasonal change in the avian hippocampus is relatively recent. There are changes in the avian hippocampus associated with seasonal food storing (Sherry and Hoshooley, 2009, 2010), seasonal reproductive behaviour (Srivastava and Singh, 2012), and annual migration (LaDage et al., 2010). Here, we will review what is known about seasonal change in the hippocampus of birds and

highlight some promising avenues for further research on the control and function of seasonal change in the avian hippocampus.

1.2. The avian hippocampus

The avian hippocampus is a dorsomedial forebrain structure (Fig. 1). Although two structures, the hippocampus and the area parahippocampalis (APH), are identified in some early atlases (Karten and Hodos, 1967) these two regions are now usually treated as a single structure – the hippocampus, hippocampal formation or hippocampal complex – and a different nomenclature is used for proposed subdivisions (Atoji and Wild, 2006). The hippocampus is bounded by the surface of the brain, the lateral ventricle, and two cytoarchitectural boundaries, one ventrally with the septum and another laterally with the hyperpallium apicale (HA, Sherry et al., 1989). The septal boundary is a cell-poor region in which fibre bundles predominate. The lateral boundary is characterised by a change in cell number and cell type from the large dispersed neurons of the hippocampus to the more cell-dense HA in which both large and small cells occur (Krebs et al., 1989). The caudal limit of the hippocampus is the caudal pole of the avian brain. The rostral boundary is more problematic. It is, by convention, associated with the first appearance (progressing rostro-caudally through the brain) of a ventral hippocampal structure consisting of densely packed cells in a V-shape that occurs though most of the hippocampus. These cytoarchitectural features characteristic of the passerine hippocampus are shown in Fig. 1 and can be seen in the

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online zebra finch atlas <http://zebrafinch.brainarchitecture.org/introduction/>.

The hippocampus has afferent and efferent connections to many other parts of the brain, including the contralateral hippocampus through the pallial commissure. Major afferent and efferent connections with forebrain areas enter and leave the hippocampus at the lateral boundary with HA. These afferents provide the hippocampus with highly processed visual, auditory, olfactory, somatosensory and trigeminal inputs (Atoji and Wild, 2006). Connections with other brain areas also occur through the septum, descending efferent projections predominating.

There are a number of proposed anatomical homologies between the avian and mammalian hippocampus (e.g. Szekely, 1999; Kahn et al., 2003; Erichsen et al., 1991). Atoji and Wild (2006) propose a homology between the V-shaped region of the avian hippocampus and the mammalian dentate gyrus, between the central region of the avian hippocampus and the mammalian CA cells fields and subiculum, and between the most lateral part of the avian hippocampus and the mammalian entorhinal cortex.

There are homologies between the hippocampus of birds and mammals in function as well as anatomy. Lesions to the hippocampus produce deficits in cache recovery and spatial orientation in food-storing birds (Krushinskaya, 1966; Sherry and Vaccarino, 1989; Hampton and Shettleworth, 1996). Hippocampal lesions disrupt memory and a variety of cognitive processes in pigeons (Good and Macphail, 1994; Scarf et al., 2014; Broadbent and Colombo, 2000; Colombo et al., 1997). Lesions also produce a complex pattern of navigational impairments in homing pigeons (Gagliardo et al., 2004). Hippocampal lesions disrupt acquisition of the ability to home from novel release sites in naïve homing pigeons but not accurate homeward orientation in experienced birds (Bingman et al., 1990, 1984). Homing pigeons with hippocampal lesions do, however, show impairments in recognition of familiar landmarks near their home loft (Bingman et al., 1984). In general, the hippocampus appears to play a role in memory for spatial locations, spatial orientation, and other cognitive processes comparable to that of the mammalian hippocampus.

Estrogen receptors, androgen receptors and aromatase are all found in the passerine hippocampus (Hodgson et al., 2008; Metzdorf et al., 1999; Gahr et al., 1993; Saldanha et al., 1998). The high level of aromatase activity, found in both sexes, indicates that estrogens produced locally in the hippocampus play an important role in the function of the avian hippocampus, as they do in the mammalian hippocampus (Saldanha et al., 1998). Aromatase is co-localised with NMDA glutamate receptors in the avian hippocampus (Saldanha et al., 2004). NMDA receptor-expressing neurons are particularly prominent in both the ventrolateral and the dorsomedial arms of the V-shaped region. Administration of estrogen increases the size of NMDA receptor-expressing neurons and the number of synaptic contacts with NMDA receptor-positive axons (Saldanha et al., 2004).

Saldanha et al. (1998) have proposed that high levels of aromatase in the hippocampus of food-storing birds may function to maintain estrogen-dependent hippocampal activity in a manner that is non-sex-specific in autumn and winter when gonadal steroidogenesis is low or non-existent. Consistent with this hypothesis is the finding that local application to the hippocampus of the aromatase inhibitor ATD (1,4,6-androstatriene-3,17-dione) causes an increase in errors on a spatial memory task in male zebra finches that is very similar to the effects of ibotenic acid lesions of the hippocampus (Bailey et al., 2013). In addition, implants of estradiol lead to more rapid learning of a spatial task in gonadectomized male zebra finches (Oberlander et al., 2004).

The hippocampus of food-storing birds, homing pigeons, and brood parasites differs from the hippocampus of other birds. The hippocampus is larger in food-storing birds, such as chickadees

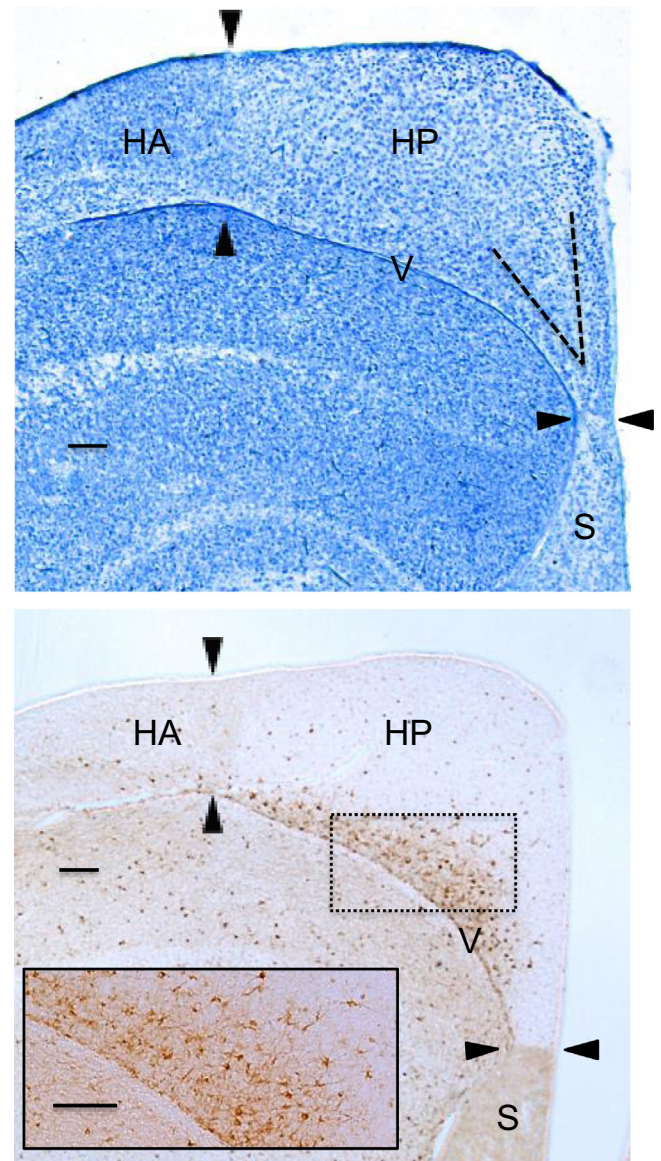


Fig. 1. Upper. The left hippocampus of the black-capped chickadee in Nissl stained coronal section. Arrowheads show the lateral boundary of the hippocampus with the hyperpallium apicale and the ventral boundary with the septum. Dashed lines indicate the location of cells forming the hippocampal "V", that appears lateral to the left arm of the dashed V and medial to the right arm of the dashed V. Lower. The left hippocampus of the black-capped chickadee showing doublecortin (DCX) immunoreactivity. Doublecortin is expressed by new neurons following cell division and during migration and differentiation. Inset shows at greater magnification the proliferative subependymal zone indicated by the dotted rectangle. Abbreviations: HA – Hyperpallium apicale, HP – Hippocampus, S – Septum, V – Ventricle. Scale bars equal 200 μ m. Photomicrographs courtesy of Adam Piraino and Caroline Strang.

and tits, nuthatches, and jays than in non-food-storing species (Sherry et al., 1989; Krebs et al., 1989; Lucas et al., 2004). It is also larger in homing pigeons than in non-homing strains (Rehkämper et al., 1988). Brood parasitic birds that search for host nests in which to lay their eggs have a larger hippocampus than closely-related non-parasites (Reboreda et al., 1996; Sherry et al., 1993). Brood parasitic brown-headed cowbirds (*Molothrus ater*), for example, have a larger hippocampus than non-parasitic red-winged blackbirds (*Agelaius phoeniceus*) and common grackles (*Quiscalus quiscula*) despite being smaller in size and having forebrains that are approximately the same size (Sherry et al., 1993). Finally, migratory subspecies of some birds can have a larger

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