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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 Hodós, 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 rostral-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

hippocampus, relative to the size of the telencephalon (Pravosudov et al., 2006), and a greater density of hippocampal neurons (Cristol et al., 2003) than non-migratory subspecies. Differences in the hippocampus between species that are correlated with differences in spatial behaviour also occur in mammals (Jacobs et al., 1990; Jacobs and Spencer, 1994; Sherry et al., 1992).

1.3. Seasonality, photoperiodism and the annual cycle

Almost every habitat on earth undergoes seasonal changes, and most species exhibit physiological, morphological, and behavioural changes in response. Seasonality in birds has been well studied, in part because birds exhibit conspicuous changes across their annual cycle. Seasonal reproduction occurs as a result of organisms matching the production of offspring with seasonal abundance of resources offspring require. In birds, the resource most important for seasonal reproduction is food. Although food is the ultimate factor (*sensu* Baker, 1938) underlying seasonal reproduction, most species use other environmental cues as proximate factors to time seasonal changes in behaviour and physiology. In seasonally breeding birds, the environmental cue most commonly used to time both reproduction and migration is the seasonal change in photoperiod (Dawson et al., 2001). Endogenous circannual timers are synchronised by the change in photoperiod to regulate seasonal changes in reproduction and migration (MacDougall-Shackleton et al., 2015). Other cues, such as temperature, weather, and social factors typically have a modulatory effect on the main photoperiod-driven changes (Wingfield, 1983; Ball, 1993).

In seasonally-breeding birds long-day photoperiods have a stimulatory effect on reproduction (reviewed in Dawson et al., 2001). In many species this termination of reproduction by the onset of photorefractoriness is absolute and may occur even prior to the summer solstice. In other species that breed opportunistically photorefractoriness may be reduced or absent, but even in these species a photoperiod response may occur (e.g. Hahn, 1998; Bentley et al., 2000).

Seasonal changes in the brain of songbirds primarily occur in response to seasonal changes in photoperiod that drive seasonal changes in gonadal steroid hormones (Tramontin and Brenowitz, 2000). This has been most extensively studied in the song-control system of songbirds. Indeed, the song-control nucleus HVC exhibits extreme seasonal plasticity (Brenowitz, 2004, 2008) and testosterone treatment is sufficient to induce an increase in HVC size (Brenowitz and Lent, 2002). However, photoperiod can also have effects on HVC that are independent of gonadal steroids (e.g. Bernard et al., 1997; Hall and MacDougall-Shackleton, 2012; Robertson et al., 2014). These gonad independent effects may potentially be driven by other hormones such as melatonin (Bentley, 2001). The consensus view, however, is that much of the seasonal plasticity observed in the song-control system results from seasonal changes in hormones that are driven by photoperiod and other factors. How photoperiod and hormones may drive seasonal changes in the avian hippocampus and hippocampus-dependent behaviour is less clear (see below).

2. Food-storing birds

2.1. Hippocampal neurogenesis

Like most members of the chickadee and tit family, the Paridae, black-capped chickadees (*Poecile atricapillus*) store food intensely during the fall and winter and much less frequently during spring and summer (Brodin, 2005; Sherry and Hoshoooley, 2007), although the details of this annual pattern can be variable (Pravosudov, 2006). Some properties of the hippocampus of chickadees,

likewise, change seasonally in a fashion that is correlated with the seasonal occurrence of food-storing behaviour. Anat Barnea and Fernando Nottebohm colour banded black-capped chickadees, injected them with [H^3] thymidine to label dividing cells, and then released them back into the wild (Barnea and Nottebohm, 1994). They were able to recapture 27 birds six weeks later. Because the initial injection of [H^3] thymidine had occurred at different times of year, and because six weeks allowed enough time for cells that initially divided in the subependymal zone (Fig. 1) to migrate into the hippocampus and mature into a neuronal phenotype, the results gave a picture of seasonal hippocampal neuronal recruitment in the wild in this food-storer. Chickadees injected in October had significantly more labelled neurons in the hippocampus at re-capture six weeks later than birds injected in August or February–March. The total number of neurons in the hippocampus did not vary seasonally. The results also showed many fewer labelled neurons in the hyperpallium apicale (HA) adjacent to the hippocampus than in the hippocampus and no seasonal pattern in the labelling of HA cells. A comparison with other chickadees recaptured after intervals longer than 6 weeks showed that the number of surviving labelled cells decreased substantially over subsequent weeks and that this effect was greater in the rostral than in the middle or caudal hippocampus. This indicates that hippocampal neurogenesis in chickadees is part of a process of neuronal turnover rather than a progressive increase in the number of neurons in the hippocampus (Barnea and Nottebohm, 1994).

The peak in 6-week survival of new neurons produced in October corresponds roughly to the early part of the food storing season for chickadees, suggesting that this peak in neuronal recruitment might be related to hippocampal involvement in caching and cache retrieval. Food caching by chickadees begins in early autumn and continues through the winter. Barnea and Nottebohm's (1994) results show that new neurons born in October are more likely to survive into November or early December than new neurons born at other times of year. Chickadees and other food-storing birds retrieve cached food by remembering the spatial locations of caches (Sherry, 1984; Vander Wall, 1982; Shettleworth and Krebs, 1982; Sherry et al., 1981; Kamil and Balda, 1985) and memory for cache sites is hippocampus-dependent (Sherry and Vaccarino, 1989; Krushinskaya, 1966; Hampton and Shettleworth, 1996). Food-storing birds have a larger hippocampus than birds that do not store food (Sherry et al., 1989; Krebs et al., 1989; Lucas et al., 2004). There are, however, a variety of other seasonal changes occurring in autumn that might affect the chickadee brain in addition to food storing (Barnea and Pravosudov, 2011). Chickadees' social system, home range, diet, and the appearance of their habitat, for example, all change in autumn at about the same time food storing begins.

To determine whether seasonal change in hippocampal neurogenesis was specifically associated with food storing, we compared two species of birds, house sparrows (*Passer domesticus*) and black-capped chickadees which both experience seasonal change of various kinds in autumn, but only one of which – chickadees – stores food (Hoshoooley and Sherry, 2007). Neither house sparrows nor chickadees are migratory and in fall, both species experience a change in their social system as breeding pairs form dominance-structured winter flocks (Smith, 1991; Lowther and Cink, 2006). The home range of individuals of both species also increases at this time. Their diets change as insect food becomes less abundant, and the appearance of the habitat changes as deciduous trees lose their leaves and snow cover becomes more frequent. We injected birds with the cell division marker bromodeoxyuridine (BrdU) at two times of year, October–November and February–April, held them in captivity for 6 weeks in large outdoor aviaries exposed to natural photoperiod and temperatures, and then counted the number of labelled neurons in the hippocampus and hyperpallium apicale. The period of time between injection and sacrifice was thus the

same as in the Barnea and Nottebohm (1994) study, but birds were held in captivity outdoors between injection and sacrifice, not released back into the wild.

We found that chickadees had much higher levels of neuronal recruitment into the hippocampus than house sparrows but there was no seasonal change in neuronal recruitment in either species. There was no species difference or seasonal difference in neuronal recruitment into HA. We also found that chickadees had a significantly larger hippocampus and significantly more hippocampal neurons than house sparrows, even though house sparrows are larger birds (mean weight 27.4 g compared to 10.6 g for chickadees) with a significantly larger telencephalon. Unexpectedly, chickadees in this study had a larger hippocampus and a greater number of hippocampal neurons in February–April than in October, evidence against the idea that seasonal change in the hippocampus is specifically associated with food storing.

These results show that food-storing chickadees have greater recruitment of new neurons into the hippocampus (and a larger hippocampus) than a non-storing species that shares some features of habitat and natural history with chickadees, but the results gave no indication of a seasonal change in the recruitment of new neurons into the hippocampus in chickadees.

To better understand the seasonal pattern of hippocampal neurogenesis in black-capped chickadees in the wild, we collected chickadees at four times of year (October, January, April and July), injected them with BrdU on the day following capture and held them in captivity for observation of food-storing behaviour for one week before sacrifice (Hoshooley et al., 2007). One week allows enough time for newly divided BrdU-labelled cells to move out of the subependymal zone into the hippocampus. We found the greatest number of labelled neurons in the hippocampus in January, an intermediate number in April and the fewest in October and July (Hoshooley et al., 2007). There were no significant differences among the four groups in the number of BrdU-labelled cells found within the subependymal zone, indicating that mitotic activity did not vary seasonally. Instead, survival of new cells in the hippocampus was the neurogenic process that varied seasonally, in this case exhibiting a peak in January. These results are much more like those obtained originally by Barnea and Nottebohm (1994) than those we obtained in our comparison of house sparrows and chickadees (Hoshooley and Sherry, 2007) but with a notably offset maximum in neurogenesis: January instead of October.

Recruitment of new neurons into the hippocampus – that is, migration, differentiation, incorporation and survival of new neurons – is the critical variable in these studies because new undifferentiated cells are generated in the subependymal zone at about the same rate year-round (Hoshooley and Sherry, 2004). Neurogenesis is a multi-step process. New cells are produced by the division of stem cells that have many characteristics of glial cells in the subependymal zone of the avian brain and migrate out of this region into forebrain sites. Some follow radial glial processes away from the ventricle into telencephalic brain areas, others migrate tangentially, parallel to the ventricular wall (Garcia-Verdugo et al., 2002; Doetsch, 2003). Seasonal differences in hippocampal neurogenesis are thus seasonal differences in recruitment, not seasonal differences in the birth of new neurons. Cellular and functional explanations for seasonal neurogenesis must therefore account for why new neurons are more likely to survive and incorporate into the hippocampus at certain times of year than others. Although seasonal changes in neuron survival and incorporation are loosely correlated with seasonal changes in food storing, this relationship has been found to be variable across studies: one report of greatest 6-week survival of neurons produced in October (Barnea and Nottebohm, 1994), one of greatest 1-week survival of neurons produced in January (Hoshooley et al., 2007) and one of no seasonal maximum in neuronal survival at all (Hoshooley and Sherry, 2007).

As described earlier, photoperiod drives the changes in gonadal steroid hormones that cause seasonal change in the song-control system of the songbird brain. Photoperiodism in black-capped chickadees is much less studied than in other songbird species, such as European starlings. Black-capped chickadees do develop absolute photorefractoriness; that is, following extended photostimulation with long-day photoperiods birds become insensitive to the stimulatory effects of long days and regress their gonads (MacDougall-Shackleton et al., 2003a,b). At this time even 24 h light will not further stimulate reproductive function (Phillimore et al., 2005) and like many other songbirds chickadees appear to require exposure to short-day photoperiods in order to reinstate photosensitivity. Although the timing of the transition from a photorefractory to photosensitive state in free-living chickadees is not known, the observed peaks in hippocampal neurogenesis reported above all occur in autumn or mid-winter when the photophase is short. At this time chickadees have completely regressed gonads (Phillimore et al., 2006) and elevated plasma melatonin levels (B. Kriengwatana and S.A. MacDougall-Shackleton, unpublished data). There is, thus, an association between hippocampal plasticity, low levels of sex steroids, and elevated levels of melatonin. Clarifying what role, if any, these hormones play in the seasonal changes observed in hippocampus, however, requires further study.

2.2. Hippocampal volume

At about the same time Barnea and Nottebohm (1994) were examining seasonal neurogenesis in food-storing chickadees, Tom Smulders et al. (1995) were investigating seasonal change in the size of the hippocampus in chickadees in the wild. They found that the hippocampus reached a maximum size in October, which, like the maximum 6-week survival of neurons produced in October described by Barnea and Nottebohm (1994), corresponds roughly to the early part of the food-storing season. The septum, a major efferent path from the hippocampus, follows the same pattern of seasonal change in size (Shifflet et al., 2002).

The increase in hippocampal volume in October is accompanied by an increase in the total number of hippocampal neurons (Smulders et al., 2000). In both adults and juveniles more large neurons occur in the hippocampus in October than at other times of years, and more small cells – some of which are neurons and others glia – are likewise found in the hippocampus in October.

Subsequent studies of wild-caught birds produced varying results. In one study, we found no difference in hippocampal volume of chickadees among the months of October, November, January and February/March (Hoshooley and Sherry, 2004). In another, we found no difference in hippocampal size among birds collected in October, January, April and July (Hoshooley et al., 2007). In a final study, we found that chickadees had a larger hippocampus from February to April than from October to November (Hoshooley and Sherry, 2007). Our birds and those collected by Smulders et al. (1995) came from the same latitude (Ithaca NY 42°26'N; London ON 42°59'N) and the same temperate North American mixed forest region. It is possible that differences among these studies are the result of sampling effects. The samples collected could, for example, contain different proportions of age classes. Alternatively, the seasonal pattern in both hippocampal neurogenesis and hippocampal volume may vary from year to year at the same latitude and in the same habitat. Many factors affect food storing by chickadees and tits. Food availability, food predictability, winter temperature, population size and many other factors could potentially affect how much food is stored in a particular season. If food-storing experience affects neurogenesis and size of the hippocampus, then year-to-year variation in these neuroanatomical variables could be the outcome (discussed further in Section 2.4).

2.3. Photoperiod and the hippocampus

Incorporation of new neurons into the song control nuclei of songbirds shows a clear seasonal pattern and is under photoperiod control (Tramontin and Brenowitz, 2000). It might therefore seem likely that seasonal recruitment of new neurons into the hippocampus is also under photoperiod control, but this turns out not to be the case. Experimental manipulations of photoperiod – switching birds from long summer day lengths to fall day lengths or vice versa – affect food storing behaviour but do not result in change in the hippocampus.

2.3.1. Photoperiod effects on food storing

Shettleworth et al. (1995) compared food hoarding in groups of captive chickadees removed from the wild at two times of year. They found that for birds captured in early spring, holding birds for six weeks at a long day summer photoperiod (18:6 h L:D at 22 °C) resulted in more food storing when these birds were then placed on a short day winter photoperiod (8:16 h L:D at 17 °C) than did holding birds throughout the experiment on a short day winter photoperiod (8:16 h L:D at 17 °C). That is, experiencing a summer photoperiod as birds would normally do before the onset of the fall food-storing season resulted in greater storing when birds were then exposed to a winter photoperiod, compared to experiencing a continuous winter photoperiod.

Birds brought into captivity in November initially stored more food than birds in the previously described groups. For these birds, holding them for 11 weeks on a short day winter photoperiod (6:18 h L:D at 18 °C) resulted in no difference in food storing when the birds were then placed on a long day summer photoperiod (16:8 h L:D at 22 °C), compared to birds held on long days (16:8 h L:D at 22 °C) throughout the experiment (Shettleworth et al., 1995). This sequence of short followed by long day lengths would normally precede spring and might be expected to cause a decrease in food storing, but this did not occur. Some manipulations of photoperiod, specifically moving birds from long days to short days, can thus affect food storing while others do not. It is also possible, however, that the temperature at which the birds were held could have affected these results (Shettleworth et al., 1995).

We manipulated photoperiod to simulate the increase in day length that might be expected to terminate food storing in black-capped chickadees in spring (MacDougall-Shackleton et al., 2003a,b). To ensure that birds were in the appropriate photosensitive state to respond to changes in day length, we held some birds on long summer days (19:5 h L:D) to establish photorefractoriness and other birds on short winter days (8.75:15.25 h L:D) to establish photosensitivity. Half of these photosensitive birds were then photostimulated by a transfer to a long day (19:5 h L:D) photoperiod. We confirmed that the photostimulation manipulation was successful by determining that it produced an increase in gonad size in both males and females. We found, however, that short days resulted in more food storing than long days, regardless of photoperiodic state or gonadal development. That is, photorefractory birds on long days throughout the experiment and photosensitive birds switched to long days stored relatively little food compared to birds held on short day lengths (Fig. 2).

It is possible that day length has the effect it has not because it induces photoperiodically-controlled physiological changes but simply because short days provide less opportunity for feeding and this causes birds to increase their food storing. Birds may interpret a shorter period of food availability in the day as a less reliable food resource and hedge their bets by food storing (Hurly, 1992; Lucas and Walter, 1991; McNamara et al., 1990; Sherry, 2014; Pravosudov and Grubb, 1997; Lucas et al., 1993). This seems not to be the case however. Karpouzou et al. (2005)

Fig. 2. Photosensitive birds (□) maintained on a short day photoperiod store more food than photorefractory (●) birds maintained on long days. Photostimulated birds (▲) decrease their storing when switched from short days to long days. Phases 1 and 2 refer to initial and final photoperiod conditions for birds held continuously on short days, continuously on long days, or switched from short to long days. Reprinted with permission from MacDougall-Shackleton et al. (2003b).

manipulated food availability and day length independently and found that while these factors influenced body weight and fat scores in black-capped chickadees, making food available for only 9 h on 15:9 h L:D or 9:15 h L:D photoperiods did not increase food storing. Similarly, making food unpredictable by randomly varying when during the day it will be available, does not affect the amount of food stored (Pravosudov and Clayton, 2001). Making food unpredictable in this way does increase the accuracy of cache retrieval, although it is not clear whether this is the result of increased attention, motivation or memory. There was no effect observed on the size of the hippocampus or the total number of hippocampal neurons in these birds (Pravosudov et al., 2002).

2.3.2. Photoperiod effects on the hippocampus

Taken together, the results described above suggest that photoperiod can affect some aspects of food storing behaviour, particularly its onset in the fall (Shettleworth et al., 1995). What about the hippocampus? Krebs et al. (1995) followed a procedure very similar to that of Shettleworth et al. (1995) and found similar effects of photoperiod on food storing (birds on short day photoperiods stored more if they had previously experienced a long day photoperiod) but there was no effect of this photoperiod manipulation on the volume of the hippocampus. MacDougall-Shackleton et al. (2003a,b) found, likewise, that the photoperiod manipulations they performed had no effect on hippocampus volume. Hoshooley et al. (2005) maintained birds on a short day photoperiod (8:16 h L:D) for several months, then switched all birds to long days (15:9 h L:D). This manipulation was confirmed to induce gonadal growth. When these birds became photorefractory after several months, half were switched to short days (8:16 h L:D) while the others remained on long days. These manipulations had no effect on the size of the hippocampus or recruitment of new neurons into the hippocampus (Hoshooley et al., 2005). Thus photoperiod manipulations that successfully induce changes in food-storing behaviour have been found not to cause changes in the hippocampus.

2.4. Experience and the Hippocampus

What should be made of the marked variability in the observed pattern of seasonal change in hippocampal neurogenesis and the absence of photoperiod effects on the hippocampus? One

possibility is that food-storing behaviour itself influences hippocampal neuronal recruitment and that year-to-year variation in food-storing behaviour is the cause of the observed differences between studies. In the song control system, singing behaviour and the neural activation of singing increases neuronal recruitment and the size of song nuclei (Alvarez-Borda and Nottebohm, 2002; Larson et al., 2013; Sartor and Ball, 2005; Ball et al., 2004). If storing or retrieving caches has similar effects, one would predict that manipulating food-caching behaviour should drive changes in the hippocampus. Food-caching behaviour has been shown to affect development of the hippocampus in young marsh tits (Clayton, 1995), but it does not appear to affect the size of the hippocampus in adult food storers (Cristol, 1996).

Captivity reduces the size of the hippocampus in food-storing and non-storing birds (Smulders et al., 2000; LaDage et al., 2009; Tarr et al., 2009; Freas et al., 2013). Holding birds in captivity could be the reason that a mixed pattern of results was found in the studies of seasonal change in hippocampal volume described earlier. If captivity reduces hippocampal size, it could attenuate naturally occurring variation in hippocampal size and mask seasonal change. Interestingly, captivity reduces the size of the hippocampus without affecting the number of hippocampal neurons (Freas et al., 2013; Roth et al., 2012; LaDage et al., 2009). Captivity can probably be considered an enforced reduction in food storing behaviour and so may provide evidence that food-storing experience has effects on the hippocampus (as well as introducing a confounding variable to studies of the avian hippocampus LaDage et al., 2009; Smulders et al., 2000; Day et al., 2008; Roth et al., 2012). In the first description of seasonal hippocampal neurogenesis in food-storing birds Barnea and Nottebohm (1994) found that captive birds showed much reduced levels of neurogenesis (but still exhibited seasonal variation in rates of neurogenesis). We found that the number of BrdU labelled cells in the chickadee hippocampus decreased over a period of weeks in captivity as the time between injection of BrdU and sacrifice increased (Hoshooley and Sherry, 2004).

It is also possible that the effect of captivity on neurogenesis and hippocampal volume is caused by stress. Both acute and chronic stress reduce cell proliferation in the hippocampus of mammals (Schoenfeld and Gould, 2012). In food-storing mountain chickadees (*Poecile gambeli*), however, elevation of corticosterone of approximately 140% above baseline for 49 days using corticosterone implants resulted in no difference in hippocampal volume, neuron number or ventricular cell proliferation rates between implanted birds and controls (Pravosudov and Omanska, 2005). Roth et al. (2012) found that chickadees that were hand-raised in captivity had the same numbers of hippocampal neurons and the same rates of hippocampal neurogenesis as wild birds, which may indicate that stress is the cause of observed reductions in neurogenesis in adults birds captured in the wild and brought into captivity.

Exercise might also be involved in the captivity effects described above. Recent evidence from European starlings (*Sturnus vulgaris*) indicates that exercise increases neurogenesis in birds (Hall et al., 2014) as it does in mammals (van Praag, 2008). Starlings that flew in a wind tunnel for several hours per day for 15 days showed elevated hippocampal neurogenesis compared to control birds that did not fly. Vitamin E has a neuroprotective effect in the rat hippocampus (Ferri et al., 2003). In starlings, enriching the starlings' diet with vitamin E increased hippocampal neurogenesis in birds that did not exercise but decreased hippocampal neurogenesis in birds that did. On the whole, it appears quite possible that the variation among studies of seasonal change in the hippocampus of food-storing parids is the result of experience-dependent effects of several different kinds, including the intensity of food-storing behaviour, and stress or the amount of exercise in captivity.

3. Brood parasites

There are five brood-parasitic species of cowbirds in the genus *Molothrus* in the New World blackbird family Icteridae. Females of the most common North American cowbird, the brown-headed cowbird (*M. ater*), search for host nests unassisted by males. Because they lay their eggs very early in the day (Rothstein et al., 1984; Scott, 1991), they are thought to lay in nests they have discovered one to several days previously. Female brown-headed cowbirds perform better than males on tests of spatial ability (Guigueno et al., 2014). Females also track the number of eggs in potential host nests in order to lay before the host has completed its clutch and begun incubation (White et al., 2009). The shiny cowbird (*Molothrus bonariensis*) is a generalist parasite like the brown-headed cowbird and is found in much of South America, the Caribbean and parts of Florida. Female shiny cowbirds perform better than males in a food search task in which the correct location is indicated with a contrasting colour cue but do not differ from males when the same task must be solved by remembering a spatial location (Astié et al., 1998).

Female brown-headed cowbirds have a larger hippocampus than males, a sex difference not found in another closely-related Icterid, the red-winged blackbird (Sherry et al., 1993). Similar sex differences in the hippocampus have been found in South American cowbirds, associated with the sex difference in search for host nests (Reboreda et al., 1996). In the generalist parasite, the shiny cowbird, only females search for host nests and females were found to have a larger hippocampus than males. In a specialist parasite, the screaming cowbird (*Molothrus rufoaxillaris*), in which both males and females search for host nests, there was no sex difference in relative hippocampal size. In the non-parasitic bay-winged cowbird (*Agelaioides badius*), no sex difference in hippocampal size occurred. This result – a sex difference in hippocampal size associated with search for host nests by females that is absent in two other cowbird species – was not observed, however, in a subsequent study of the same three species (Nair-Roberts et al., 2006).

There may be seasonal change in the size of the cowbird hippocampus (Clayton et al., 1997). Clayton et al. (1997) found that both males and females of the generalist shiny cowbird had a larger hippocampus in the breeding season than in the non-breeding season and females had a relatively larger hippocampus than males. No statistical interaction between sex and season is reported but the authors state that a sex difference in relative hippocampal size present during breeding is absent in non-breeding. Both males and females of the specialist parasite, the screaming cowbird, had a larger hippocampus in the breeding season than in the non-breeding season but there was no difference in hippocampus size between the sexes. A seasonal change in relative size of the hippocampus such as this could account for the difference in results, described above, obtained by Reboreda et al. (1996) and Nair-Roberts et al. (2006). Clayton et al. (1997) are cautious in their conclusions regarding seasonal differences, however, noting that seasonal comparisons of this kind can be confounded by seasonal differences in the populations from which samples are drawn. The non-breeding population, for example, may contain more young birds with a developmentally different hippocampus. Nevertheless, these results do provide some indication that there may be seasonal change in the hippocampus that is associated, like food storing, with seasonal change in the cognitively demanding and possibly hippocampus-dependent behaviour of searching for and remembering host nests.

4. Reproduction

Srivastava and Singh (2012) have reported substantial increases in the thickness of dendrites and the number of dendritic spines of

hippocampal neurons in breeding compared to non-breeding condition in the ringneck parrot (*Psittacula krameri*). They examined Golgi-stained pyramidal, multipolar, bipolar and unipolar cells in the APH region of the hippocampus and found the dendrites of all four cells types to be thicker in birds collected during the breeding season. Dendritic spine density was, similarly, elevated in most cells types in breeding birds (Srivastava and Singh, 2012). A comparable change in the density of apical dendritic spines of CA1 pyramidal cells over the estrous cycle – specifically, lowest spine density during estrus – has been observed in rats (Woolley et al., 1990). The spacing between hippocampal cells also increases during breeding in the ringneck parrot, perhaps as a consequence of the change in density of dendritic spines (Singh and Srivastava, 2013). Srivastava and Singh (2012) note that there are a variety of changes in behaviour, cognition, and affect associated with breeding in birds that may recruit the functions of the hippocampus or alter hippocampal structure.

5. Migration

Changes in the hippocampus are associated with migration in a number of species. Some of these effects appear to be a consequence of migratory experience rather than recurring seasonal phenomena of the kind seen in food-storing birds or in association with reproduction. The available evidence, nevertheless, shows that migration is associated with hippocampal plasticity in birds and may provide avenues for further research on the causes of seasonal change in the hippocampus.

Healy et al. (1996) found that age and migratory experience both produced an increase in relative hippocampal size in garden warblers (*Sylvia borin*) and that older experienced birds had more hippocampal neurons than younger inexperienced birds. In non-migratory Sardinian warblers (*Sylvia melanocephala*) age did not affect hippocampal size. Migratory and non-migratory subspecies of the dark-eyed junco (*Junco hyemalis hyemalis* and *J. h. carolinensis*, respectively) do not differ in the size of the hippocampus but migrants have a greater density of hippocampal neurons (Cristol et al., 2003). Hippocampal volume was found to be greater in migratory Gambel's white-crowned sparrow (*Zonotrichia leucophrys gambelii*) than in non-migratory Nuttall's white-crowned sparrow (*Z.l. nuttalli*) (Pravosudov et al., 2006). As with garden warblers, age also affected hippocampal size. Adults had a larger hippocampus than juveniles in both subspecies, adult migratory Gambel's had a larger hippocampus than adult non-migratory Nuttall's, and within juveniles there was a larger left but not right hippocampus in migratory Gambel's compared to non-migratory Nuttall's. Adult Gambel's also had more neurons in the right (but not the left) hippocampus compared to Nuttall's (Pravosudov et al., 2006). Finally, adult migratory Gambel's white-crowned sparrows were found to have a greater level of neurogenesis than non-migratory Nuttall's white-crowned sparrows while no difference was observed in juveniles (LaDage et al., 2011). This effect, interestingly, appears to be due to a developmental decrease in neurogenesis in non-migrants from the juvenile to the adult stage that does not occur in migrants.

There has been no research testing specifically for annual variation in the hippocampus of migratory birds. Effects observed in the studies described above are consistent with the hypothesis that, in addition to changes in the hippocampus due to age, migratory experience causes a one-time change in the hippocampus that persists throughout adulthood (and such a change is, naturally, absent in non-migrants). It would be valuable to determine whether there are annual cyclic changes in the hippocampus of migrants in advance of, during, or following migration.

6. Seasonal change in the mammalian hippocampus

A variety of rodents exhibit naturally occurring seasonal change in the hippocampus (Yaskin, 2011). For voles and shrews, this can involve a reduction of 30% or more in the total size of the hippocampus in winter, a change that occurs in other forebrain regions, too, but primarily affects the hippocampus (Yaskin, 2011). The summer increase in size of the hippocampus is correlated with an increase in spatial range, especially in males (e.g. Yaskin, 2013). Rates of neurogenesis also vary seasonally in wild populations of voles, with females showing higher levels of cell proliferation than males and higher levels during non-breeding than during breeding (Galea and McEwen, 1999; Omerod and Galea, 2003). In Richardson's ground squirrel (*Urocitellus richardsonii*) the size of the dentate gyrus and the rate of hippocampal neurogenesis both vary seasonally (Burger et al., 2014) but such seasonal effects do not occur in grey squirrels (Lavenex et al., 2000a,b).

Hormonal control of neurogenesis in the rodent hippocampus has been extensively investigated (reviewed in Galea et al., 2013). Estrogens and androgens affect the hippocampus in a sex-specific fashion. Estradiol increases cell proliferation and cell survival in female rats. It has little effect on male rats or mice but can increase cell survival in male voles during a specific limited phase of cell maturation. Androgens increase cell survival in male rodents but have no effect on cell proliferation (Galea et al., 2013).

The hormonal control of adult neurogenesis in mammals, particularly rodents, presents a complex picture and relatively few studies specifically examine seasonal change in the hippocampus in wild populations. What is clear, however, is that hormones interact in a complex fashion with experience, sex and season in the regulation of naturally-occurring change in the mammalian hippocampus and that the potential for investigating hormonal control of seasonal change in the avian hippocampus has been, by comparison, largely untapped.

7. Conclusions

The avian hippocampus undergoes seasonal change most clearly in food-storing birds, although it has also been described in brood parasites and occurs in association with breeding in some species. Changes in the hippocampus are associated with migration, too, but it is not clear whether or not these changes are a recurring seasonal phenomena. Photoperiod, which has a strong and pervasive effect on the hormonal control of seasonal change in the song control system of songbirds, has been shown to have no effect on seasonal change in the hippocampus of food-storing birds although it can induce change in food-storing behaviour. This photoperiod independence suggests that seasonal change in the hippocampus of food-storing birds may be a consequence of food-storing behaviour itself. Year-to-year variation in the timing of seasonal change in hippocampus size and hippocampal neurogenesis also supports this suggestion. The hypothesis that seasonal variation in the hippocampus of food-storing birds is a consequence of seasonal variation in food storing is, however, by no means proven. Patterns of seasonal variation in the hippocampus are highly variable and are found in some properties of the hippocampus and not others. A number of factors associated with captivity, including the amount of food storing behaviour that can occur in captivity, stress, and exercise also complicate interpretation of results on seasonal change in the hippocampus of food storing birds. In addition, although both food storing and seasonal change in the hippocampus tend to occur in fall and winter rather than spring and summer, the temporal relation between them is not strong.

Hormonal control of change in the hippocampus has been extensively examined in mammals, particularly changes associated

with the reproductive cycle of male and female rodents. Although food-storing occurs in the non-breeding season in most food-storing birds and there are no sex differences in food-storing or the hippocampus in black-capped chickadees (Petersen and Sherry, 1996), the avian hippocampus is rich in aromatase and both estrogen and estradiol cause structural change in the avian hippocampus and hippocampus-dependent behaviour of birds. Hormonal control of hippocampal plasticity in mammals may provide a useful model and source of hypotheses for examining seasonal hippocampal plasticity in birds.

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