

Review

The seasonal hippocampus of food-storing birds

David F. Sherry*, Jennifer S. Hoshoooley

Department of Psychology and Program in Neuroscience, University of Western Ontario, London, ON, Canada N6A 5C2

ARTICLE INFO

Article history:

Received 13 June 2008

Received in revised form 13 December 2008

Accepted 15 December 2008

Keywords:

Food storing
Hippocampus
Neurogenesis
Seasonality
Spatial cognition
Black-capped chickadee

ABSTRACT

Food storing is seasonal in birds like chickadees, nuthatches and jays, occurring at high levels in fall and winter and low levels in spring and summer. Memory for cache sites is hippocampus dependent in chickadees and both the recruitment of new neurons into the hippocampus and the total size of the hippocampus change seasonally. Unlike seasonal change in the vocal control nuclei of songbirds, however, change in the hippocampus appears not to be controlled by photoperiod. The annual timing of hippocampal neuronal recruitment and change in hippocampal size is quite variable, reaching maximum levels at different times of year in different studies. The amount of food-storing activity by chickadees is known to be influenced by flock dominance structure, energy balance, food availability, and other seasonally varying factors. The variable timing of seasonal change in the hippocampus may indicate that the hippocampus of food-storing birds changes annually in response to change in the intensity of food storing behaviour itself.

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Contents

1. Food-storing chickadees and non-storing sparrows	335
2. The annual timing of food storing and change in the hippocampus	336
3. What do new hippocampal neurons do?	337
4. Conclusions	337
References	337

Black-capped chickadees begin caching food in early fall, continue through the winter and cache very little at all during summer. Chickadees store seeds and insect prey in hundreds to thousands of individual sites in bark crevices, under lichen, and between conifer needles (Odum, 1942; Petit et al., 1989; Haftorn, 1974; Brodin, 2005). Stored food is retrieved by remembering the spatial locations of scattered caches (Shettleworth, 1990; Sherry, 2006; Smulders and DeVoogd, 2000; Sherry and Hoshoooley, 2007). Food storing by chickadees can be both a short- and long-term proposition. Direct monitoring of caches made by chickadees and their close relatives in the family *Paridae*, the European tits, shows that stored food is sometimes retrieved on the same day it was stored and most caches are recovered within a few days (Cowie et al., 1981; Stevens and Krebs, 1986). Experiments with radio-labelled stored food, however, show that cache retrieval can also occur after much longer intervals, as much as 30 days after storing (Brodin and Ekman,

1994). Chickadees probably use a dual strategy when storing food from a rich source like a feeder, harvesting most caches very quickly while leaving others for longer periods and perhaps re-storing some retrieved food in new caches. Both short- and long-term hoarding serve to reduce variation in food availability, either within-day on a time scale of hours or within-season on a time scale of many weeks.

Accurate cache retrieval is hippocampus dependent in chickadees (Sherry and Vaccarino, 1989; Hampton and Shettleworth, 1996). The hippocampus of food-storing birds is also relatively larger than the hippocampus of non-food-storing species (Krebs et al., 1989; Sherry et al., 1989; Lucas et al., 2004). Two remarkable discoveries show that not only does food storing vary seasonally but the hippocampus itself changes seasonally too. Barnea and Nottebohm (1994) found a seasonal pattern in the recruitment of new neurons into the hippocampus of black-capped chickadees that, like food-storing behaviour, reaches a maximum in fall, at about the time seasonal food storing begins. New neurons are born in the subventricular zone and migrate, probably following radial glial processes, into the hippocampus (Fig. 1A). There is a very high level of attrition of these new neurons and few survive for long. Operationally, neuronal recruitment refers to the continuing pres-

* Corresponding author. Tel.: +1 519 661 2111x84659; fax: +1 519 661 3961.
E-mail address: sherry@uwo.ca (D.F. Sherry).

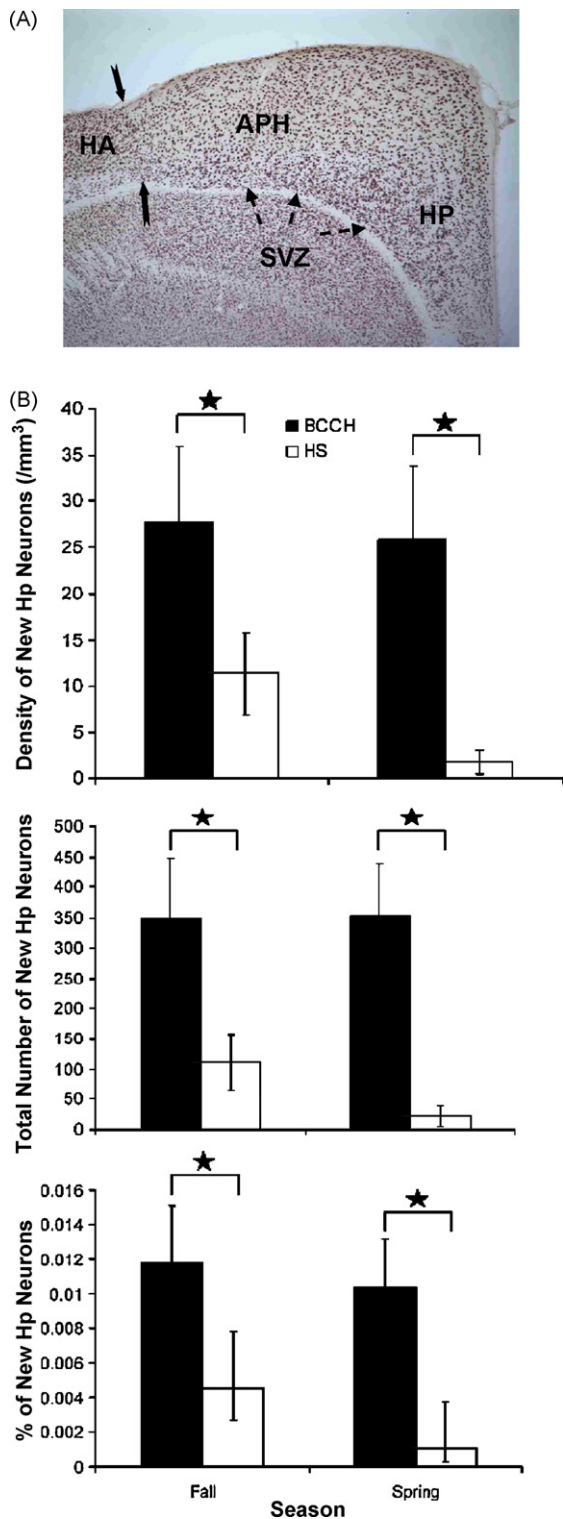


Fig. 1. (A) The chickadee hippocampus consists of the hippocampus proper HP and the area parahippocampalis APH. New neurons are born in the subventricular zone SVZ (dashed arrows) and migrate into the hippocampus. Solid arrows show the boundary between the hippocampus and hyperpallium accessorium HA. This coronal section of the left hippocampus is labelled for the neuronal nuclei specific protein NeuN. 5 \times objective magnification. (B) The hippocampus of black-capped chickadees (BCCH) has significantly more new neurons than the hippocampus of house sparrows (HS) in both fall and spring whether measured as the density of new neurons (upper), the number of new neurons (middle), or the percentage of hippocampal neurons that are new (lower). Error bars equal \pm 1SEM, * p < 0.05. Redrawn from Hoshoooley and Sherry (2007) by permission of John Wiley & Sons, Inc.

ence in the hippocampus of neurons labelled at an earlier point in time with a cell-birth marker such as tritiated thymidine or bromodeoxyuridine (BrdU). Cell-birth markers are incorporated into the nucleus of dividing cells during the S-phase of mitosis and the marker can later be detected by autoradiography or immunocytochemistry. In Barnea and Nottebohm's study, cells undergoing division in fall were found 6 weeks later in the hippocampus – by this time with a neuronal phenotype – at a higher rate than cells labelled at other times of year. During the 6 week interval between administration of the cell-birth marker and neuroanatomical analysis, labelled cells migrated into the hippocampus and developed into mature neurons.

In a parallel study, Smulders et al. (1995) found that the size of the hippocampus changed seasonally, occupying about 4% of the forebrain in February, increasing to 5.5% in October, an increase of nearly 40%. Smulders et al. (1995) suggested that this increase in the size of the hippocampus may be caused by increased use of the hippocampus to retrieve stored food. Many seasonal changes in the avian brain are controlled by photoperiod, but change in hippocampal neuronal recruitment and hippocampal size is not. Manipulations of day length that cause increases and decreases in food storing in captive birds have no effect on either neuronal recruitment (Hoshoooley et al., 2005) or hippocampal size (Krebs et al., 1995; MacDougall-Shackleton et al., 2003) even though these same manipulations of daylength are sufficient to induce moult and to bring males and females into breeding condition.

These results raise a number of questions about seasonal plasticity in the hippocampus of food-storing birds that we attempted to answer using a combination of behavioural and neuroanatomical approaches. The first was, is the seasonal pattern in recruitment of new neurons into the hippocampus restricted to food-storing birds, or is it found in other songbirds, too? Another question was, what precisely is the temporal relation between food-storing behaviour and change in the hippocampus? According to Pravosudov (2006), we may know less than we think about seasonal patterns in food storing by chickadees and tits. Pravosudov surveyed all of the available data on seasonal variation in food storing by chickadees and tits in the wild and found considerable variation not only between species but also from year to year in the same species at the same study site. While some studies show a clear autumn peak, others show an elevated rate from late summer through the fall and sometimes an additional peak in food storing in the spring. Pravosudov concluded that environmental, social and climatic factors that affect food availability and energy balance probably determine the timing and intensity of food storing in any given year. It may therefore be significant that while some of the studies of hippocampal size described above found seasonal changes (Smulders et al., 1995), others did not (Barnea and Nottebohm, 1994; Hoshoooley and Sherry, 2004). The production of new neurons in the subventricular zone and the first occurrence of these cells in the hippocampus show little seasonal variation (Hoshoooley and Sherry, 2004; Hoshoooley et al., 2007) implying that whatever triggers the long-term incorporation of new neurons into the adult hippocampus has a relatively stable and abundant supply of new neurons to work with. Hippocampal seasonality may potentially be as variable as the seasonality of food storing itself.

1. Food-storing chickadees and non-storing sparrows

If seasonal neurogenesis in the hippocampus of adult chickadees is an adaptation for remembering large numbers of cache sites, or even caused by remembering large numbers of cache sites, it should not occur in birds that do not store food. Although maxima in hippocampal neuronal recruitment and food storing both occur in the fall, chickadees experience a number of other changes in fall, too, that could quite reasonably place additional demands

on memory and the hippocampus. The social system of chickadees changes in fall from breeding pairs to winter flocks that average about eight individuals (Smith, 1991). Chickadee diet also changes as insects become scarcer and harder to find in autumn. The size of the home range increases about three-fold from the spring and summer breeding territory to the winter flock territory. Finally, the appearance of the habitat changes dramatically as deciduous trees lose their leaves and the landscape becomes covered in snow. Fortunately for comparative purposes there are a variety of non-migratory species of birds in regions where chickadees are common that do not store food. We compared black-capped chickadees and house sparrows because both undergo comparable changes in autumn in their social system, diet, home range size, and appearance of their habitat and both are abundant. House sparrows are larger than chickadees and come from a different family of birds, the Old World sparrows or *Passeridae* but most importantly, they do not store food. A comparison of hippocampal neurogenesis in chickadees and house sparrows thus controls for a number of seasonal changes that coincide with the onset of food storing in chickadees.

In both fall (October to November) and spring (end of February to mid-April) chickadees showed about 3.5 times more hippocampal neuronal recruitment than did house sparrows, whether this was measured as the number of new neurons, new neurons per cubic millimetre, or the proportion of all hippocampal neurons that were new (Hoshoooley and Sherry, 2007, Fig. 1). There was no indication, however, of seasonal change in neuronal recruitment in either species. This result clearly differs from earlier results that found significantly higher levels of recruitment in October than in February/March (Barnea and Nottebohm, 1994). In a neighbouring area of the brain, the hyperpallium accessorium (Fig. 1A), there was no difference in neuronal recruitment between chickadees and house sparrows and no indication that neuronal recruitment differed between fall and spring in this region in either species. This shows that chickadees do not exhibit, overall, more incorporation of new neurons in the adult brain. Instead, the observed differences between food-storing chickadees and house sparrows were specific to the hippocampus.

The hippocampus was significantly larger in chickadees than in house sparrows and had a greater total number of neurons even though house sparrows are larger and have a larger forebrain. The hippocampus was also larger, relative to the size of the forebrain, in spring than in fall in chickadees but in house sparrows there was no seasonal change in relative hippocampal size. This result – greater hippocampal size in spring than in fall in chickadees – contrasts with previous results that found an October maximum in hippocampal size in chickadees (Smulders et al., 1995).

Chickadees and house sparrows differ in many ways, not just food storing. They differ in evolutionary history and house sparrows, because of their larger size, may differ in their winter energetics from chickadees. Unfortunately for comparative purposes, all North American chickadees and titmice store food (Sherry and Hoshoooley, 2007), so the ideal comparison of chickadees that store food and chickadees that do not is not possible. What our comparison of chickadees and house sparrows does show, however, is that the larger hippocampus occurs in the smaller food-storing bird and that this hippocampus undergoes the greater amount of neuronal recruitment. Furthermore, the heightened level of neuronal recruitment occurs specifically in the hippocampus and not in all areas of the forebrain.

2. The annual timing of food storing and change in the hippocampus

The chickadees in the previous study were held in captivity for 6 weeks between administration of the cell-birth marker BrdU and

sacrifice, to permit a comparison with previous research that also allowed 6 weeks for new neurons to mature and migrate into the hippocampus. Captivity, however, reduces hippocampal neuronal recruitment (Barnea and Nottebohm, 1994; Hoshoooley and Sherry, 2004). Our sampling periods were also quite broad, around 40 days. In addition, we had no direct observations of caching behaviour in the previous study to compare to our observations on change in the hippocampus. For these reasons, we examined in a subsequent study neuronal recruitment much sooner after capture in chickadees taken from a population of individually color-banded chickadees living in the wild. We were able to sample at more time points – October, January, April and July – and because the birds had previously been banded we were able to ensure our samples included only adults one year of age or older (Hoshoooley et al., 2007). Birds were given BrdU on the day following capture then held in captivity for 7 days to permit observations of food-storing behaviour before sacrifice.

More birds captured in October stored food than birds captured at other times of year. The highest level of hippocampal neuronal recruitment was found in the January sample, the next greatest in April, with relatively low levels observed in both October and July (Fig. 2). These results are similar to those of an earlier study in which a January peak in BrdU labelling, albeit a non-significant one, occurred in birds collected at four time points between Octo-

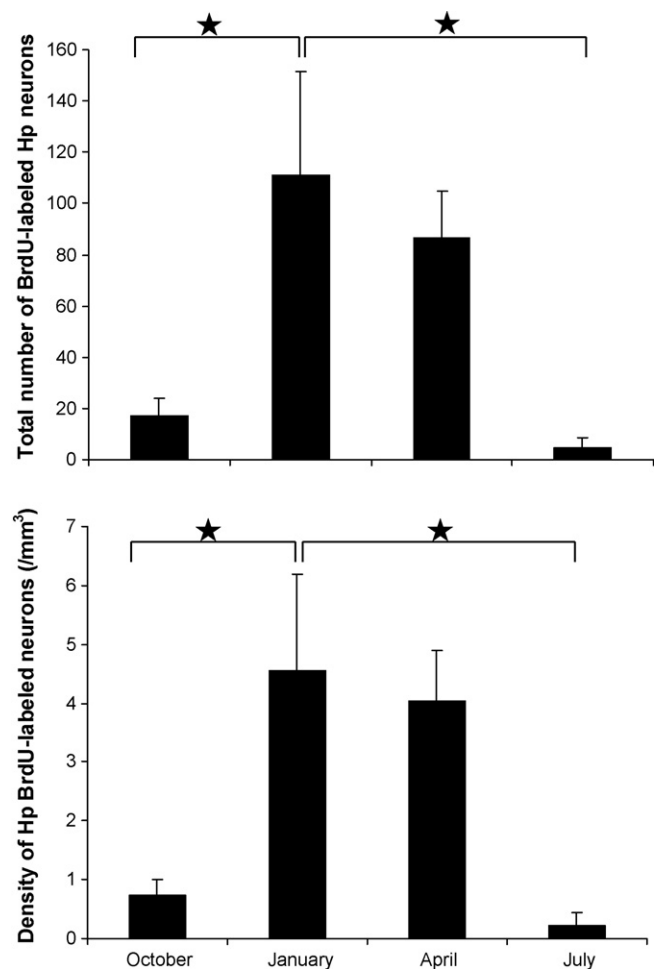


Fig. 2. New neurons occur in the hippocampus of black-capped chickadee at a higher rate in January than in either October or July, with an intermediate level of occurrence in April. Upper panel shows the number of new hippocampal neurons labelled for the cell-birth marker BrdU and the lower panel the density of new neurons. Error bars equal ± 1 SEM, * $p < 0.05$. Redrawn from Hoshoooley et al. (2007) by permission of S. Karger AG, Basel.

ber and March (Hoshoooley and Sherry, 2004). No seasonal change was observed in mitotic activity in the subventricular zone adjacent to the hippocampus where new hippocampal neurons originate, confirming that it is not cell division but the survival of these new neurons in the hippocampus that varies seasonally. Finally, we found no seasonal change in either hippocampal size or size of the hippocampus relative to the rest of the forebrain, in contrast to earlier results (Smulders et al., 1995).

The general picture that emerges from these results is that the seasonal timing of hippocampal neurogenesis is variable and that seasonal change in total hippocampal size is detected in some studies and not others. One explanation for these seemingly contradictory outcomes may be that “season” is not the best predictor of change in the chickadee hippocampus. Expectations about seasonal change in the brain of food-storing birds are derived in part from what is known about the vocal control nuclei of songbirds. Although there is considerable variation among species in the annual pattern of change in these nuclei, one conclusion that holds in most cases is that increasing day length sets in motion a number of changes in the brain and behaviour of photosensitive birds that lead to song production, mating and reproduction (Tramontin and Brenowitz, 2000). In males, these changes include growth of the gonads, an increase in the circulating level of testosterone, the onset of song, and a marked increase in size of the vocal control nuclei HVC and RA. The song system may not, however, be the best model for annual change in the hippocampus. Attempts to induce change in hippocampal neurogenesis and hippocampal size by manipulations of photoperiod have not produced the effects on the hippocampus that such manipulations produce on the vocal control nuclei.

An alternative hypothesis may better describe annual change in the hippocampus. It is known that food storing by chickadees and tits is sensitive to energy balance, food availability, food predictability, and flock dominance structure (Brodin and Lundberg, 2003; Lucas et al., 1993; Lucas and Walter, 1991; Hurly, 1992). If change in the hippocampus is caused, even in part, by feedback from food-storing behaviour itself, then we would expect year-to-year variation in both food-storing and the hippocampal response to this behaviour. In juvenile marsh tits one to two months old, food storing experience increases hippocampal neurogenesis (Patel et al., 1997). In adults, dominant flock members have higher rates of hippocampal cell proliferation than subordinates (Pravosudov and Omanska, 2005). Dominance structure, flock demographics, energy balance, ambient temperature, food availability and other physical, biotic, and social factors may all influence food-storing behaviour and hence the timing and magnitude of hippocampal neuronal recruitment. Such causal complexity presents many challenges to researchers but may be a more realistic model of annual change in the hippocampus of food-storing birds. In fact, recent research suggests that singing behaviour may have a greater influence on morphological change in the song control nuclei than previously suspected (Sartor and Ball, 2005). In starlings, dominant males sing more than subordinate males. Sartor and Ball placed male starlings in pairs in order to establish dominance relations and thereby influence song production. The song control nucleus HVC was significantly larger in males that sang more, suggesting that singing behaviour, along with known neuroendocrine affects, causes change in size of the song control nuclei.

3. What do new hippocampal neurons do?

Despite the current level of interest in adult neurogenesis in the hippocampus of birds and mammals, there is little consensus about the function of adult generated hippocampal neurons (Gahr et al., 2002; Kempermann, 2002; Bruel-Jungerman et al., 2007). Most new hippocampal neurons do not survive long. Their high

rate of attrition, comparable to the rates of attrition that occur in the brain early in development, suggests that new neurons survive only when they encounter the appropriate conditions, which quite likely include incorporation into functional circuits. One model, proposed by Fernando Nottebohm, is that new memories require new neurons in both in the vocal control nuclei (Goldman and Nottebohm, 1983), and the hippocampus (Barnea and Nottebohm, 1994). This is of course quite different from the idea that change in synaptic connectivity is sufficient to process or store new information. The hippocampus is generally viewed as a processing station for the storage and retrieval of memory, not a site of long term storage, and so the “new neurons for new memories” hypothesis must describe why information processing by the hippocampus requires new neurons. Perhaps new neurons are involved in short-term retention in the hippocampus, or are assigned a retrieval function when memory is consolidated for long-term storage outside the hippocampus.

One very interesting observation is that immature neurons have properties not found in mature neurons. New neurons have larger action potentials, respond differently to some neurotransmitters, and have longer lasting long-term potentiation (Doetsch and Hen, 2005; Gould et al., 1999). Perhaps there are special functions for cells with such properties in the hippocampus, and new neurons must continually be added because these properties are lost as the neurons mature.

4. Conclusions

The hippocampus of food-storing birds is plastic, showing annual variation in both neuronal recruitment and total size that is not seen in species that do not store food. The timing of these changes, however, is variable and not under direct photoperiodic control. Variability in annual timing of hippocampal change may occur because the hippocampus responds to variation in the intensity of food-storing behaviour and its associated demands on memory. The explanation for variability in the timing of annual change in the hippocampus may lie in year-to-year variation in flock structure, food availability, ambient temperature and other factors that exert their influence of food-storing behaviour.

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