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The Hippocampus of Food-Storing Birds

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The classic paper discussed in this essay:
Sherry DF, Vaccarino AL, Buckenham K, Herz RS (1989): The hippocampal complex of food-storing birds. Brain Behav Evol 34: 308-317.

In 1984–1985, Anthony Vaccarino and I performed a number of experiments on the effects of hippocampal lesions on the accuracy of cache recovery in food-storing black-capped chickadees [Sherry and Vaccarino, 1989]. Like most research, the genesis of this project involved many people. I presented a poster on memory for cache sites at the Neurobiology of Learning and Memory meeting in Irvine, Calif. in 1984 and Larry Squire pointed out to me that the obvious next experiment was to test for hippocampal involvement. I mentioned this idea to my friend Michael Leon at the same meeting, noting that I had no experience doing neurosurgery on 11-gram passerine birds and Michael, with his usual aplomb said that was no problem, there were colleagues at my own institution, the University of Toronto, like Alison Fleming, who could easily teach me the surgical skills.

Alison introduced me to Anthony, who was working in Alison's lab as an undergraduate, and we were on our way. We found that hippocampal lesions severely disrupted the ability of chickadees to find their caches. Fortunately for us, the birds continued to make caches and search for them, they just searched in the wrong places. This work formed part of Anthony's undergraduate thesis and we published the paper in *Behavioral Neuroscience* in 1989 [Sherry and Vaccarino, 1989].

We had used the Stokes, Leonard and Nottebohm canary brain atlas [Stokes et al., 1974] as a guide to lesion placement but when we examined sections from our control birds we saw something very striking. The hippocampus was clearly much larger in chickadees than shown in the atlas. Where the canary atlas showed a smooth curve as the dorsal surface of the brain travelled medially and descended between the hemispheres, the chickadees had a large bump. Previous work by many researchers on the songbird brain had prepared us for the idea that regions of the bird brain could vary between species. Song control nuclei vary in relative size between species and it seemed a likely hypothesis that food-storing birds, which can remember the spatial location of thousands of scattered food caches, might have a hippocampus that was bigger than the hippocampus of non-storing birds.

With help from the Long Point Bird Observatory in Ontario, Anthony and I began collecting food-storing and non-storing birds, sectioning the brains and measuring the relative size of the hippocampus. I contacted my former postdoctoral supervisor at Oxford, John Krebs, and John proposed that his team would collect European species in a parallel project.

In Canada, Anthony and I, with help from George Wallace and the banders at Long Point, were able to collect individuals of 23 species from 3 food-storing families (chickadees, nuthatches and jays) and 10 non-food-storing families and subfamilies (wrens, kinglets, thrushes, mimids, starlings, warblers, cardinals, buntings, finches, and Old World or 'true' sparrows). With help from Karen Buckenham and Rachel Herz we sectioned the brains, projected images of each section onto paper with a slide enlarger, and traced the outlines of the hippocampus, telencephalon, and other prominent structures. I then traced the outline of the hippocampus and forebrain using a Numonics digitizing tablet attached to an Apple IIe computer running Jandel software. I remember calibrating the tablet each time by determining the area of a square with side length equal to a scale bar we had traced onto each sheet along with the section drawing. I combined the area estimates and inter-section intervals into volume estimates (using the formula for the volume of a truncated cone kindly provided by Alasdair Houston) and plotted the volume of the hippocampus relative to the volume of the forebrain.

The results were clear. Food-storing birds had a larger hippocampus, relative to telencephalon size, than did non-storing species over a wide range of brain size. We repeated our statistical analysis sorting birds into other categories that might have an influence on relative hippocampus size – migrant/non-migrant, solitary/social, omnivore/dietary specialist – and found that none of these variables accounted for significant variation in relative hippocampus size in the way that the storer versus non-storer distinction did. Our sample included eight long-distance migrants that differ substantially in the distance travelled on their annual migratory

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flight, but we found no relation between relative hippocampus size and migratory path length. We presented the results at the 1988 meeting of the Society for Neuroscience in Toronto [Sherry et al., 1988] and submitted our 'citation classic' to *Brain, Behavior and Evolution* in April 1989 [Sherry et al., 1989]. Although this was one of the early manifestations of 'neuroecology' – exploring the effects of ecological selection pressures on the brain and behaviour – I am pleased to see on re-reading the paper that our conclusions were in fact quite balanced: 'Although the discussion has stressed that the observed differences are the result of natural selection, this does not discount the possibility that individual experience in storing and retrieving food may play a role in the development of this size difference in the hippocampus' (p. 316).

Meanwhile, I had travelled to Oxford to consult with John and with Hugh Perry who were providing neuroanatomical expertise in Oxford. Sue Healy, who was a graduate student with John at the time, and I traced some sections together to confirm that we were going about things in the same way. The work on European species, with a few North American species and cage birds added for good measure, was submitted and published the same year [Krebs et al., 1989].

Looking back, I am struck by three things. The first is how primitive our methods were not so very long ago. Apple IIe computers are practically unknown today except to vintage computing enthusiasts. I can clearly remember the squeaking sound of popping the plastic cover off to insert the communication card for the digitizing tablet. The second thing that strikes me is how much time we devoted to verifying that this structure we were calling hippocampus really was 'hippocampus'. I pored over classic sources on avian neuroanatomy [Rose, 1914; Craigie, 1930; Ariëns Kappers et al., 1936; Källén, 1962] and searched the contemporary literature [Benowitz and Karten, 1976; Krayniak and Siegel, 1978; Casini et al., 1986] for evidence of true homology, evidence that the mammalian hippocampus and the avian hippocampus were derived with modification from a structure in their most recent common ancestor. In the end, the evidence from several sources was quite compelling. I did not realize until later that one of the authorities I was reading, Edward Horne Craigie [Craigie, 1930], was still living and was Professor Emeritus in the University of Toronto Department of Zoology. Craigie had worked with Ramon y Cajal and in 1937 had translated Cajal's autobiography into English.

As it turned out, the avian and mammalian hippocampuses develop from the same embryonic pallial precursors. The distribution of neurotransmitters and connectivity to other brain regions, likewise, provide convincing evidence of homology. I recall that when giving talks on this work, the first question was often, 'What makes you think it is hippocampus?', a variant on another question I used to get when first talking about our work on memory for food caches [Sherry et al., 1981; Sherry, 1984]: 'What makes you think it is memory?'

Finally, the comparative methods we used were very elementary compared to statistical comparative methods that are now routine. We followed recommended methods in use at the time [Harvey and Mace, 1982], but phylogenetic comparative methods have moved on considerably since then [Stone et al., 2011].

We and others followed up these results with comparative analyses of relative hippocampus size in food-storing corvids, migrants, and brood parasites [Healy and Krebs, 1992; Sherry et al., 1993; Basil et al., 1996; Healy et al., 1996]. One interesting development was a re-analysis of existing data by Anders Brodin and Ken Lundborg that appeared to show that despite our earlier conclusions, there was in fact no consistent relation between food-storing behaviour and relative hippocampus size in birds [Brodin and Lundborg, 2003]. Brodin and Lundborg were looking at a slightly different question than we had originally. We had compared families of birds in which most member species were food storers to families and subfamilies in which no species stored food. Brodin and Lundborg compared species within the Parid family (chickadees and tits) and within the Corvid family (jays and crows) that differed in how much they stored food. They found no significant relation between hippocampus size and food storing in either family. It seemed quite possible that because of shared phylogeny, there might indeed be little variation in relative hippocampus size within food-storing families. This result prompted further re-analyses, however, to which Anders Brodin also contributed, confirming our original findings [Garamszegi and Eens, 2004; Lucas et al., 2004; Garamszegi and Lucas, 2005]. These re-analyses showed that hippocampus size is significantly correlated with the intensity of food-storing behaviour even within the Paridae and Corvidae and that the same pattern holds in comparisons between food-storing and non-storing families of birds. Remarkably, these studies also found a consistent difference in hippocampus size between North American and Eurasian species, with Eurasian birds having larger hippocampuses, even among non-storing species.

It has been very gratifying to see how research on the brain of food-storing birds has developed from these first results. New researchers have joined the field and work in the area has expanded to address a variety of new questions, described in a recent theme issue on the ecology, psychology and neurobiology of food hoarding [Pravosudov and Smulders, 2010].

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