Food storing and the hippocampus in corvids: amount and volume are correlated

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SUMMARY

The volume of the hippocampal region (dorsomedial cortex) relative to body mass was measured in seven species of corvid (red-billed blue magpie, *Cissa erythrorhyncha*; European crow, *Corvus corone*; rook, *C. frugilegus*; jackdaw, *C. monedula*; jay, *Garrulus glandarius*; magpie, *Pica pica*; and Alpine chough, *Pyrrhocorax graculus*). The species studied differ in the extent to which they store food, and the results showed that there is a positive correlation between the estimated amount of food-storing behaviour and the relative volume of the hippocampus among the seven species. For two of the species, magpie and jackdaw, intraspecific variation was analysed. These two species show a sex difference in relative hippocampal volume (males larger than females), although there are no reports of sex differences in storing behaviour. In the magpie, which stores food regularly, hippocampal volume relative to body mass is positively related to relative volume of the rest of the telencephalon, whereas in the jackdaw, which rarely stores food, there is no relation.

1. INTRODUCTION

Most members of the passerine family Corvidae store food (Goodwin 1986; Vander Wall 1990). However, the amount of storing varies considerably between species, as has been shown both in North America (Balda & Kamil 1989; Vander Wall 1990) and in Eurasia (Goodwin 1986). The range of observed variation encompasses species that virtually never store, e.g. the European jackdaw, *Corvus monedula* (Simmons 1968; Henty 1975; Goodwin 1986), to species in which stored food represents a modest proportion of the diet, e.g. the European crow, *Corvus corone* (Simmons 1968), European magpie, *Pica pica* (Birkhead 1991), and species in which stored food represents a major component of the diet, e.g. Clark's nutcracker, *Nucifraga columbiana* (Vander Wall 1990) and European jay, *Garrulus glandarius* (Bossema 1979). This last group of corvids also has the special feature of retrieving food many months after storage. Both Clark's nutcrackers and European jays harvest seed crops from trees in the autumn and use them the following season during the nestling period. In contrast, corvids such as magpies and crows tend to store and retrieve on a short-term basis of hours (James 1984; Birkhead 1991), to days or weeks.

This variation in food-storing behaviour within one family provides an ideal opportunity to test in more detail the relation between storing behaviour and brain specialization described for passerine birds as a whole by Krebs *et al.* (1989) and Sherry *et al.* (1989). These authors categorized passerine species as storers or non-storers, and showed that at the family or subfamily level, among the passerines, food-storing behaviour is associated with an evolutionary enlargement of the volume of the hippocampal region (dorsomedial cortex) relative to the rest of the forebrain and to body mass. The hippocampal region is known to have a role in the spatial memory used for retrieving stored food (Krushinskaya 1966, 1970; Sherry & Vaccarino 1989), and it has therefore been hypothesized that the enlargement of the hippocampal region of food-storing birds represents an adaptation associated with a specialized memory capacity for retrieving stores (Krebs 1990).

In this study we compare the hippocampal volume relative to body mass of corvids belonging to the three categories referred to above. Our analysis depends critically on distinguishing between the categories: although there are a few quantitative studies of the amount of storing, the following summarizes the available data upon which we base the categorization into three groups.

1. In seven studies that specifically report observations on food storing in corvids including jackdaws, five report no storing by adult jackdaws in the wild (Henty 1975; Goodwin 1986; Röell 1978, cited in Goodwin 1986; Waite 1985; Editor's note following Richards 1974), two report occasional storing in the nest box by captive (Lorenz 1970) or wild (Richards 1974) birds, and one reports the storage of a single item outside the box in the wild (Simmons 1968). We therefore conclude that jackdaws may be categorized as storing little or no food. Observations of Alpine choughs, *Pyrrhocorax graculus*, suggest that this species also stores very rarely (E. Gwinner, personal communication on observation by H. Schöpf: 'has studied Alpine choughs for many years but has seen food caching only 2 or 3 times';

13-2

Table 1. *Body mass, telencephalon and hippocampal volumes for the birds used in the analyses*

(All values were logarithmically transformed before analysis.)

Species	Body mass/g	Telencephalon/mm³	Hippocampus/mm³
alpine chough	163.0	36.013	0.603
carrion crow	438.3	50.574	1.332
carrion crow	395.4	49.192	1.303
jackdaw	250.0	34.075	0.639
jackdaw	200.0	31.775	0.511
jackdaw	221.9	29.063	0.680
jackdaw	210.3	29.613	0.620
jackdaw	206.6	27.616	0.617
jackdaw	216.7	25.875	0.609
jackdaw	186.6	29.066	0.552
jackdaw	221.4	29.100	0.725
jackdaw	199.7	27.260	0.609
jackdaw	217.7	34.884	0.613
jackdaw	183.2	27.377	0.709
jackdaw	213.7	26.053	0.555
jackdaw	199.6	27.497	0.626
jay	194.8	22.567	1.160
jay	190.0	23.678	1.000
magpie	221.0	34.142	1.019
magpie	224.0	34.374	1.145
magpie	191.2	27.814	0.886
magpie	170.0	25.932	0.861
magpie	164.7	28.851	1.127
magpie	177.2	28.229	0.947
magpie	188.4	32.589	1.113
magpie	180.4	30.193	1.018
magpie	186.8	25.608	0.763
magpie	162.4	27.993	0.953
magpie	178.0	28.810	0.857
magpie	178.2	27.031	0.896
magpie	152.6	29.036	1.098
red-billed magpie	202.7	32.936	0.778
rook	333.5	56.796	1.163

Strahm 1960; Thaler 1977; Delestrade, personal communication).

2. Our second category includes three species for which storing behaviour has been well documented: European crow, European magpie, and rook, *Corvus frugilegus* (Simmons 1968; Källander 1978; Birkhead 1991). A fourth species in this category included in our analysis is the widely distributed Asian red-billed blue magpie, *Cissa erythrorhyncha*, a species whose storing behaviour has not been described in detail but is referred to by Goodwin (1986) as engaging in some storing behaviour.

3. The European jay depends to a very considerable extent on stored acorns (fruit of *Quercus spp.*) throughout the winter and spring. Acorns are stored in large numbers between September and November, and Bossema (1979) found that during the winter 100% of jay stomachs examined contained acorns, and that during the breeding season 80% of nestling food samples taken in June contained acorns. In other words, jays probably retrieve their stores up to nine months after making them. Quantitative estimates of hoarding by jays suggest that each individual hoards between 6000 and 11000 seeds per year (Schuster 1950; Chettleburgh 1952).

In addition to analysing the association between food storing and relative hippocampal volume we also used data from two of the species for which the largest sample sizes were available, magpie and jackdaw, to test for sex and hemispheric differences in hippocampal volume.

2. METHODS

The study involved 33 adult (post-juvenile) individuals belonging to seven species. The sample sizes were as follows: magpie 13, jackdaw 13, European jay 2, crow 2, rook 1, Alpine chough 1, red-billed blue magpie 1 (see table 1 for raw data). With the exception of the red-billed blue magpie and Alpine chough, birds were collected from the wild between February and June. The red-billed blue magpie was purchased from an avicultural supplier, and the Alpine chough was provided by the Innsbruck Alpine Zoo. All birds were treated in the following way. Their body mass was determined after an intraperitoneal overdose of sodium pentabarbitone, and then they were transcardially perfused with heparinized physiological saline followed by 10% (by volume) formal-saline. The brains were subsequently post-fixed for approximately 7 d before being transferred to 30% (by volume) sucrose formalin. The brains were then sectioned in the coronal plane at either 25 μm or 50 μm thickness. In the former case, a 1 in 10 series was stained with a cresyl violet, in the latter a 1 in 5 series.

The areas of the hippocampal region (as characterized by Krebs *et al.* (1989) and Erichsen *et al.* (1991)) and telencephalon, excluding the hippocampal region (as defined by Karten & Hodos (1967)) were traced from the sections at 10 × enlargement, confirming all boundaries under higher magnification. These areas were subsequently digitized and volumes of the hippocampal region and telencephalon approximated by the formula for a truncated cone. The birds were sexed after perfusion by examination of the gonads.

In comparative analyses such as the one reported here, it is important to take into account phylogenetic effects that might confound other interpretations of differences between species (Harvey & Pagel 1991). To date, the phylogenetic data for the Corvidae are insufficient to determine the relatedness of genera beyond the level of the tribe. All the genera in this study belong to the same tribe, Corvini (Sibley & Monroe 1990). Because European crow and rook belong to the same genus, and are therefore likely to share characteristics on the basis of phylogenetic relatedness alone, and because they are categorized in the same food-storing group for the present analysis, the data for the two species are combined. Thus the analysis is based on six data points.

3. RESULTS

Figure 1*a* shows the relation between relative hippocampal volume and food-storing behaviour. The data were analysed by linear regression in which hippocampal volume relative to body mass was plotted against degree of food storing (scored as 1, 2 and 3 for low, medium and high storing, respectively). (The effects of telencephalon are not removed because once the effects of body mass are removed from hippocampal volume, telencephalon volume does not significantly account for any of the remaining variation in hippocampal volume). Figure 1*a* shows that there is a significant relation ($r^2 = 0.79$, $F_{1,4} = 15.57$, $p = 0.017$) between relative hippocampal volume and storing category. Figure 1*b*, *c* shows that neither body mass nor relative telencephalon volume (with respect to body mass) are correlated with amount of food storing (body mass; $r^2 = 0.02$, $F_{1,4} = 0.07$, $p = 0.80$; relative telencephalon volume; $r^2 = 0.08$, $F_{1,4} = 0.33$, $p = 0.58$). These analyses assume that the x-variable (amount of storing) can be placed on a linear scale. A more conservative analysis is to consider three categories: high, middle and low, and to calculate the probability that the largest hippocampal volume occurs in the high category and the smallest volume occurs in the low category, i.e. that there is some relation between hippocampal volume and amount of storing. With six data points, the probability that the relation we observe occurs is 0.0013 ($(1/3)^6$), whereas the probability that a relation of any sort occurs is 0.016 (there are 12 combinations which produce a linear relation, positive and negative: $12 \times (1/3)^6$). Therefore the result shown in figure 1*a* is still significant.

For two of the species, magpie (a moderate food storer in category 2) and jackdaw (a species that is virtually a non-storer in category 1), sufficient data were available to make further comparisons. The volume of the hippocampus relative to body mass differed significantly between the two species ($t = 4.58$, d.f. $= 24$, $p = 0.0001$). This confirms the overall

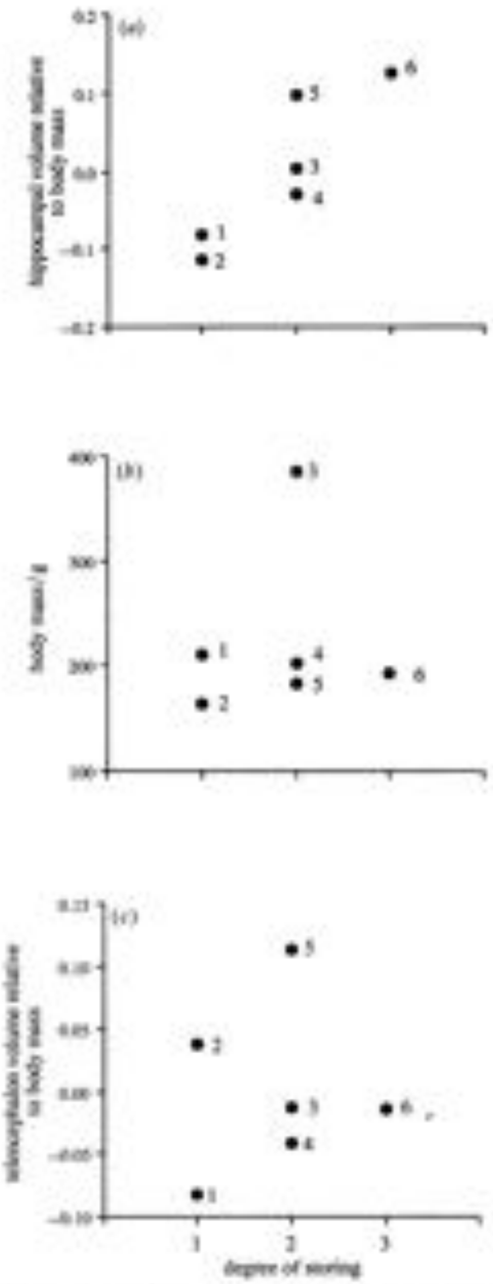

Figure 1. (*a*) Volume of the hippocampus relative to the body mass plotted as a function of category of storing behaviour. The data points are as follows: 1, alpine chough; 2, jackdaw; 3, rook and crow combined; 4, red-billed blue magpie; 5, magpie; 6, European jay. (*b*) The relation between body mass and storing and (*c*) the relation between relative telencephalon volume (to body mass) and storing. Code for figure points as in (*a*).

pattern of figure 1*a* that food storing is associated with relative hippocampal volume. More puzzling is the relation illustrated in figure 2, in which hippocampal volume relative to body mass is plotted against telencephalon volume relative to body mass. In magpies, relative hippocampus volume increases with relative telencephalon volume ($r^2 = 0.57$, $F_{1,11} =$

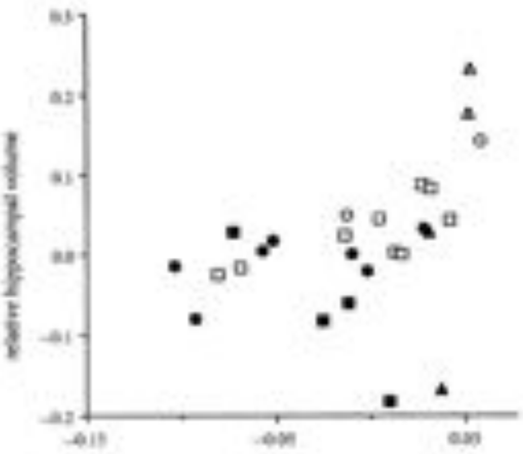

Figure 2. The relative volume of the hippocampus plotted against relative telencephalon volume for magpies (open symbols) and jackdaws (filled symbols), with males (circles), females (squares) and unsexed birds (triangles) of the two species. In magpies there is a significant positive relation, whereas in jackdaws there is no significant relation. Males have a slightly larger relative hippocampus than females (male jackdaws, $n = 7$; female jackdaws, $n = 4$; unsexed jackdaws, $n = 2$; male magpies, $n = 2$; female magpies, $n = 9$; unsexed magpies, $n = 2$). Note that the residuals (relative volumes) in the figure are not directly comparable with those in figure 1, because here the regressions from which the residuals are calculated are single-species regressions, whereas in figure 1 all species are combined.

14.31, $p = 0.005$), whereas in jackdaws there is no such relation ($r^2 = 0.001$, $F_{1,11} = 0.002$, $p = 0.97$). Figure 2 also shows that there is a slight sex difference in relative hippocampal volume in both jackdaws and magpies. In a two-way analysis of variance in which the association between both species and sex and hippocampal volume relative to both body mass and telencephalon volume was examined (both are included because both are correlated with hippocampal volume in magpies), species had a highly significant effect ($F_{1,24} = 17.93$, $p = 0.0005$), whereas sex was just significant ($F_{1,24} = 4.43$, $p = 0.049$) (four birds, (two magpies and two jackdaws) were not sexed). Males had a slightly larger relative hippocampus than females. There was no interaction ($F_{1,24} = 0.19$, $p = 0.67$). Although lateralization of function in certain brain structures associated with learning and memory in chicks has been demonstrated (Andrew 1991), in neither jackdaw nor magpie was there any difference in volume of the left and right hippocampus (jackdaws, paired $t = 0.75$, d.f. $= 12$, $p = 0.47$; magpies, paired $t = 0.15$, d.f. $= 12$, $p = 0.88$).

4. DISCUSSION

Our main result is that relative hippocampal volume amongst corvids is associated with the degree of food-storing behaviour. This result extends previous work (Krebs *et al.* 1989; Sherry *et al.* 1989) by demonstrating a graded relation between storing and brain specialization. European Jays show the most extreme hippocampal specialization of the species studied here. Jays differ from the other species both in terms of the number of items stored and in the interval between storage and retrieval, which may be as long as 9 months in jays, compared with a few hours or days in the other species. Therefore the present analysis does not distinguish between the possibilities that hippocampal enlargement is associated with duration or amount of memory for stored food.

The slight sex difference in relative hippocampal volume in the magpie and jackdaw is unexpected, as there is no evidence for sex differences in storing behaviour in any of the species of corvid or parid that have been studied to date. Jacobs *et al.* (1990) found that sex differences in home range size (and therefore perhaps spatial memory requirements) of voles was associated with a sex difference in relative hippocampal volume, but there is no evidence for sex differences in home range size of either jackdaws or magpies.

We have no explanation of the result shown in figure 2, namely that in the food-storing magpie, but not in the non-storing jackdaw, the relative volume of the hippocampus increases with relative telencephalon volume. As this pattern holds even after effects of body size have been controlled for, it cannot be explained by arguing that larger magpies need to store more food and therefore need a bigger hippocampus for processing spatial information. Two other possibilities are that the pattern relates to age or to individual variation in food-storing behaviour. S. D. Healy & J. R. Krebs (unpublished data) have shown that in the magpie, but not the jackdaw, the relative volume of the hippocampus increases with age between fledging and post-fledging birds. It is possible that this relation extends over a longer timescale, and that as birds get older both the telencephalon and the relative volume of the hippocampus increases. The other hypothesis is that individuals vary in the extent to which they store food, and that this variation is correlated both with overall telencephalon volume and relative volume of the hippocampus. This individual variation could, of course, be age related, in which case the two hypotheses would collapse into one. In either case, the association between relative hippocampal volume and telencephalon size could come about through an association between enlargement of the hippocampal region itself and enlargement of another part of the hippocampal circuit involved in spatial memory which is here classified as part of the telencephalon. In further analysis, if it proves possible to identify specific nuclei with afferent or efferent connections to the hippocampal region, it may be possible to ascertain which parts of telencephalon are correlated with hippocampal volume within magpies.

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