

Tool-Making New Caledonian Crows Have Large Associative Brain Areas

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Key Words

Brain • Brain size • Cognition • *Corvus moneduloides* • Mesopallium • New Caledonian crow • Striatopallidal complex • Tool making • Tool use

Abstract

Animals with a high rate of innovative and associative-based behavior usually have large brains. New Caledonian (NC) crows stand out due to their tool manufacture, their generalized problem-solving abilities and an extremely high degree of encephalization. It is generally assumed that this increased brain size is due to the ability to process, associate and memorize diverse stimuli, thereby enhancing the propensity to invent new and complex behaviors in adaptive ways. However, this premise lacks firm empirical support since encephalization could also result from an increase of only perceptual and/or motor areas. Here, we compared the brain structures of NC crows with those of carrion crows, jays and sparrows. The brains of NC crows were characterized by a relatively large mesopallium, striatopallidal complex, septum and tegmentum. These structures mostly deal with association and motor-learning. This supports the hypothesis that the evolution of innovative or complex behavior re-

quires a brain composition that increases the ability to associate and memorize diverse stimuli in order to execute complex motor output. Since apes show a similar correlation of cerebral growth and cognitive abilities, the evolution of advanced cognitive skills appears to have evolved independently in birds and mammals but with a similar neural orchestration.

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Introduction

Higher cognitive abilities have been linked to increased brain size in mammals. These superior abilities are reflected in different domains such as tool use [Reader and Laland, 2002], social skills [Byrne and Corp, 2004] and behavioral flexibility [Sol et al., 2008]. Higher levels of behavioral flexibility also correlate with increased brain size in birds [Portmann, 1946; Lefebvre et al., 1997; Iwaniuk et al., 2004; Cnotka et al., 2008]. The volume of certain associative pallial structures in the avian forebrain are especially good predictors of innovative foraging behavior and tool use [Timmermanns et al., 2000; Lefebvre et al., 2002, 2004; Lefebvre and Sol, 2008]. Among the class of birds

(Aves), the corvid family is especially renowned for their flexible behavior and cognitive skills [Rehkämper et al., 1991; Iwaniuk and Hurd, 2005; Sol et al., 2005]. New Caledonian (NC) crows (*Corvus moneduloides*) display extraordinary skills in making and using tools to acquire otherwise unobtainable food [Hunt, 1996; Hunt and Gray, 2003, 2004]. These birds manufacture an impressive range of both stick and leaf tools [Hunt and Gray, 2002, 2003, 2004a], may have evolved rudimentary cumulative technology [Hunt and Gray, 2003] and can bend unfamiliar material like wire into functional tools [Weir et al., 2002]. NC crows can also use one tool to get another (metatool use) [Taylor et al., 2007] and solve complex physical cognition tasks that require causal reasoning [Taylor et al., 2009]. These skills rival those of apes [Emery and Clayton, 2004; Emery, 2006].

NC crows have one of the largest avian brains for their body size [Cnotka et al., 2008]. However, when brains evolve to a larger size it is mostly by a differential increase in certain areas and not by a change in the size of all areas, which means that encephalization can result from a mosaic-like pattern of differential growth of brain components [Rehkämper et al., 2001; Iwaniuk et al., 2004; Rehkämper et al., 2008]. Thus, an investigation of the association between encephalization and cognitive skills requires the comparative analysis of separate brain structures. In a first attempt to identify which parts of the NC crow's brain are larger than in other birds, we compared the volume of 15 brain areas between NC crows and three other passerine species [carrion crows (*Corvus corone corone*), European jays (*Garrulus glandarius*) and domestic sparrows (*Passer domesticus*)]. Among birds, Passeriformes in general have relatively large brains and telencephalic volumes [Rehkämper et al., 1991; Burish et al., 2004; Iwaniuk and Hurd, 2005]. The size of the nidopallium is the best predictor of 'true' tool use [Lefebvre et al., 2002]; therefore this structure in NC crows should be relatively large when compared to non-tool users. However, the size of the mesopallium is the best predictor of behavioral innovation and flexibility generally in birds [Timmermanns et al., 2000]. The high level of tool skills in NC crows (e.g. their manufacture and use of hooks) and their demonstrated cognitive ability in tool- and non-tool-related experiments suggest that their behavior is based on a high level of cognitive ability generally. Therefore, we also predicted that the mesopallium in NC crows would be relatively enlarged. As well as the mesopallium and the nidopallium, we investigated if other associative areas such as the striatopallidal complex showed differential size increase in the NC crow.

Material and Methods

Subjects

We collected the brains of 5 NC crows (*Corvus moneduloides*), 5 European carrion crows (*C. corone corone*), 2 European jays (*G. glandarius*) and 4 sparrows (*P. domesticus*). All the animals were captured in their original habitat and weighed immediately after capture.

Brain Collection

The 16 individuals were euthanized with an overdose of pentobarbital. After cardiac arrest was confirmed, they were perfused with physiological saline solution and a fixative (Bodian's fluid). The brains were carefully dissected, weighed, sectioned and stained for perikarya. We determined total brain volume and the volume of 15 distinct areas: hyperpallium apicale, hyperpallium densocellulare, mesopallium, nidopallium, arcopallium, entopallium, striatopallidal complex (including the globus pallidus, lateral striatum, medial striatum and the tuberculum olfactorium), septum, hippocampus, bulbus olfactorius, tegmentum (this was the brain part caudal to the diencephalon including the medulla oblongata, but excluded the tectum and cerebellum), cerebellum, tectum opticum, tractus opticus and diencephalon. For carrion crows, jays and sparrows, volumetric data other than for the arco- and entopallium were taken from Rehkämper et al. [1991]; we measured the arco- and entopallium from the brain slides used in the 1991 paper.

Analyses

Net brain volume was calculated as the sum of the single brain components. In contrast to total brain volume, the net brain volume does not include the volume of leptomeninges, ventricles, choroid plexus and remains of brain nerves. The nidopallium includes the basal nucleus and field L, and the arcopallium includes the nucleus taeniae amygdalae and parts of the tractus occipitomesencephalicus.

To compare volumes of brain structures in different species with different body weights, allometric methods were used. This involved the calculation of a regression line that expressed the brain (or brain component) size/body weight relationship. We used body weight to account for body size variation because of the well-proven correlation between brain (structure) size and body weight [Snell, 1892; Dubois, 1897; Stephan et al., 1986, 1988; Rehkämper et al., 1991; Baron et al., 1996]. Alternative means of accounting for variation in body size such as using net brain volume or brain stem volume were unsuitable because we wanted to investigate possible enlargement in these parts as well.

To obtain a reliable regression slope for passerines, the body weight range between the smallest and largest species should ideally be a factor of 10; the body weight range for the four species in our study met this criteria. The species that we used to calculate the regression line were also part of a biologically appropriate group, the order Passeriformes [Sibley and Alquist, 1990]. The slopes of brain (or brain component) size/body weight relations were calculated according to the formula:

$$\begin{aligned} & \log \text{ brain (or brain component) size} \\ & = \log b + a \times \log \text{ body weight} \end{aligned}$$

where 'a' is the slope and 'b' the intersection with the y axis. Regression lines were calculated for each brain structure using data points for all 16 individuals [Warton et al., 2006].

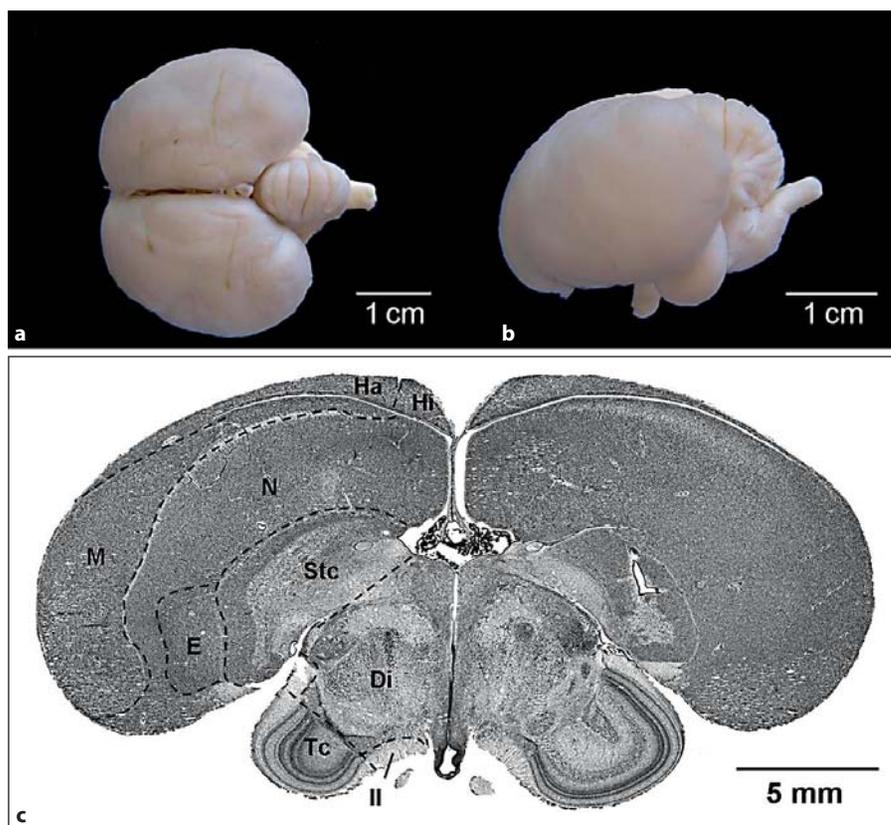


Fig. 1. The brain of the NC crow. **a, b** Lateral and dorsal view of an NC crow brain. **c** Coronal section through the brain of a NC crow to illustrate some subdivisions. Di = Diencephalon; E = entopallium; Ha = hyperpallium apicale; Hi = hippocampus; M = mesopallium; N = nidopallium; Stc = striatopallidal complex; Tc = tectum opticum; II = tractus opticus. Gallyas stain.

To test for differences in brain structure volumes between species we calculated allometric size indices (actual brain component size/expected brain component size). The indices represent the distance of individual data points from the regression line. The expected brain (or brain component) size is the value on the regression line that corresponds to a given individual body weight. The methods that we used for the preparation of brain material, establishing boundaries between brain areas, measurements and for allometric calculations are taken from the literature [Stokes et al., 1974; Stephan et al., 1988; Rehkämper et al., 1991; Rehkämper and Zilles, 1991].

To test the hypothesis that the tool use and considerable cognitive skills of NC crows are detectable in the size of associative forebrain components, we compared the allometric indices for the NC crow to: (1) the pooled data for the three other passerine species (European jays, sparrows and carrion crows), and (2) the carrion crow alone. We carried out the first comparison because we wished to compare the NC crow with passerines in general. The three species for which we pooled data are appropriate representatives of Passeriformes to compare with the NC crow since they all have relatively large brains [Portmann, 1947; Rehkämper et al., 1991; Boire and Baron, 1994]. The alternative of testing each species separately with NC crows was problematic because of low sample sizes for the European jay and the sparrow. We carried out the second comparison with the carrion crow to directly rule out that any enlargement of structures in the NC crow was due to an

evolved characteristic of the genus *Corvus* associated with generalist foraging behavior.

We tested for differences between allometric indices using *t* tests. We adjusted the α level to account for multiple pair-wise *t* tests using the Bonferroni correction; the α level was thus set to 0.025.

Results

The brain of the NC crow has conspicuously large hemispheres (fig. 1). We provide the average body weights, brain weights and brain area volumes for the four study species in table 1. The five NC crows had significantly larger allometric indices for the mesopallium ($t = 3.917$; $p = 0.002$), striatopallidal complex ($t = 4.816$, $p < 0.001$), septum ($t = 6.940$, $p < 0.001$) and the tegmentum ($t = 3.705$, $p = 0.002$) compared to the pooled data for the three other passerines (table 2). Figures 2 and 3 give the results of the comparison for the mesopallium. The nidopallium was also larger in the NC crow, but this difference was not significant with the adjusted α level ($t =$

Table 1. Volumes of brain structures (mm³) and body weight (g) in four Passeriformes species

	Sparrow (n = 4)	European jay (n = 2)	Carrion crow (n = 5)	NC crow (n = 5)
Brain volumes				
Total brain volume	954.88 ± 14.602	3,735.53 ± 245.713	9,573.53 ± 985.749	7,295.40 ± 741.105
Net brain volume	935.93 ± 13.391	3,647.91 ± 242.726	9,203.11 ± 1,025.258	7,227.89 ± 721.664
Hyperpallium apicale	91.08 ± 9.517	381.84 ± 6.364	963.22 ± 135.741	711.25 ± 118.957
Hyperpallium densocellulare	26.21 ± 5.274	57.88 ± 7.312	129.37 ± 25.310	78.82 ± 17.087
Mesopallium	100.05 ± 8.221	452.55 ± 9.489	1,397.41 ± 190.791	1,158.72 ± 121.010
Nidopallium	272.99 ± 21.755	1,106.21 ± 14.616	3,449.75 ± 447.439	2,546.55 ± 359.119
Entopallium	5.57 ± 1.140	27.33 ± 7.408	55.52 ± 7.695	42.38 ± 5.845
Arcopallium	31.48 ± 3.775	110.35 ± 4.299	266.15 ± 26.186	179.05 ± 17.703
Striatopallidal complex	97.31 ± 6.415	365.27 ± 53.217	848.23 ± 77.184	768.92 ± 60.682
Hippocampus	8.55 ± 1.025	25.74 ± 2.100	26.51 ± 7.845	29.20 ± 10.846
Septum	4.03 ± 0.130	17.12 ± 1.711	29.32 ± 3.478	42.50 ± 3.341
Bulbus olfactorius	0.48 ± 0.064	1.04 ± 0.368	2.01 ± 0.372	1.43 ± 0.382
Telencephalon	637.75 ± 28.607	2,545.26 ± 70.923	7,167.48 ± 864.597	5,558.55 ± 664.442
Diencephalon	44.93 ± 0.747	180.09 ± 32.089	283.52 ± 32.773	205.51 ± 32.683
Tractus opticus	13.25 ± 2.229	63.06 ± 22.691	126.04 ± 28.982	77.64 ± 4.442
Tectum	62.68 ± 1.142	244.67 ± 28.157	356.94 ± 49.750	303.79 ± 24.484
Tegmentum	84.42 ± 5.430	283.32 ± 50.685	500.95 ± 63.375	489.68 ± 17.613
Cerebellum	92.90 ± 10.58	331.51 ± 38.191	768.17 ± 94.855	592.74 ± 35.86
Body weight, g	27.18 ± 2.635	139.67 ± 16.447	466.73 ± 71.082	277.25 ± 29.874

Values are means ± SD.

Table 2. Allometric brain volume indices in four Passeriformes species

	S+J+C (n = 11)	Carrion crow (n = 5)	NC crow (n = 5)
Total brain volume (a = 0.822, b = 1.816)	0.96 ± 0.112	1.01 ± 0.157	1.10 ± 0.159
Net brain volume (a = 0.818, b = 1.814)	0.96 ± 0.107	0.94 ± 0.147	1.12 ± 0.161
Hyperpallium apicale (a = 0.838, b = 0.771)	0.98 ± 0.133	0.95 ± 0.133	1.09 ± 0.199
Hyperpallium densocellulare (a = 0.529, b = 0.647)	1.07 ± 0.204	1.14 ± 0.223	0.92 ± 0.249
Mesopallium (a = 0.959, b = 0.64)	0.92 ± 0.108*	0.88 ± 0.026*	1.22 ± 0.198
Nidopallium (a = 0.908, b = 1.141)	0.96 ± 0.103	0.94 ± 0.03	1.13 ± 0.217
Entopallium (a = 0.826, b = -0.42)	0.99 ± 0.170	0.92 ± 0.162	1.07 ± 0.127
Arcopallium (a = 0.748, b = 0.428)	1.01 ± 0.085	1.01 ± 0.098	0.99 ± 0.114
Striatopallidal complex (a = 0.794, b = 0.869)	0.93 ± 0.087*	0.88 ± 0.113*	1.20 ± 0.144
Hippocampus (a = 0.408, b = 0.394)	0.98 ± 0.270	0.87 ± 0.234	1.21 ± 0.503
Septum (a = 0.775, b = -0.45)	0.84 ± 0.174*	0.72 ± 0.170*	1.55 ± 0.220
Bulbus olfactorius (a = 0.482, b = -1.013)	1.04 ± 0.204	1.08 ± 0.233	0.98 ± 0.295
Telencephalon (a = 0.876, b = 1.574)	0.95 ± 0.114	0.94 ± 0.137	1.14 ± 0.189
Diencephalon (a = 0.635, b = 0.771)	1.03 ± 0.194	0.98 ± 0.183	0.99 ± 0.189
Tractus opticus (a = 0.769, b = 0.039)	1.06 ± 0.284	1.05 ± 0.357	0.95 ± 0.124
Tectum (a = 0.616, b = 0.951)	0.99 ± 0.205	0.92 ± 0.204	1.07 ± 0.110
Tegmentum (a = 0.655, b = 1.015)	0.94 ± 0.143*	0.88 ± 0.183*	1.19 ± 0.083
Cerebellum (a = 0.754, b = 0.898)	0.97 ± 0.128	0.96 ± 0.196	1.08 ± 0.060

Values are means ± SD. S = Sparrow; J = European jay; C = European carrion crow; a = slope of the regression line; b = intersection with the y-axis. Asterisks indicate significant differences versus NC crows.

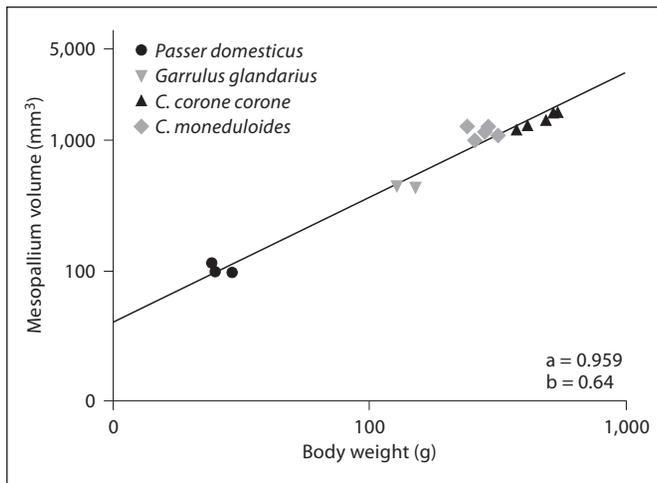


Fig. 2. Double logarithmic plot of mesopallium volume versus body weight for 16 individuals from four Passeriformes species. $a = 0.959$; $b = 0.64$.

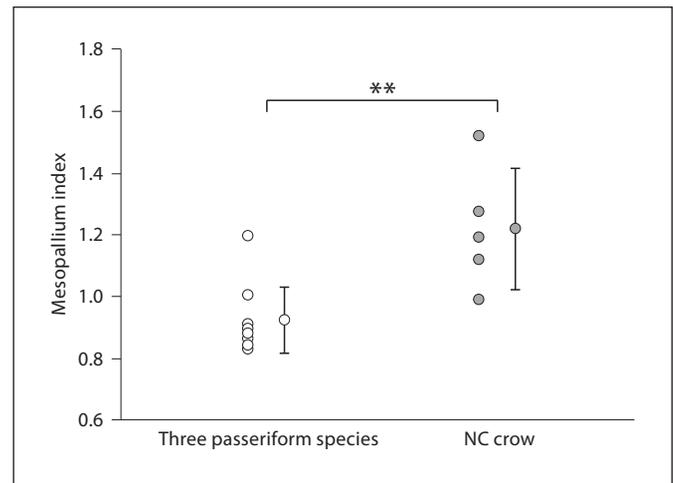


Fig. 3. Mesopallium indices for 11 individuals from three Passeriformes species (*Passer domesticus*, *Garrulus glandarius* and *C. corone corone*) compared to the indices for 5 NC crows. Individual data with means \pm SD; ** $p = 0.002$. The error bars are offset from the data points for clarity.

2.174, $p = 0.047$). The comparison with the carrion crow (*C. corone corone*) also revealed significantly larger mean indices for NC crows in the above four structures (mesopallium: $t = 3.742$, $p = 0.006$; striatopallidal complex: $t = -3.933$, $p = 0.004$; septum: $t = -6.027$, $p < 0.001$, and tegmentum: $t = -3.504$, $p = 0.008$).

Discussion

Brain Structures

We found that four brain areas in NC crows are enlarged compared to the three other passerine species: mesopallium, pallidostriatal complex, septum and tegmentum. This finding supports our hypothesis that NC crows' impressive tool and general problem-solving skills are associated with enlargement of associative and motor-related structures in the forebrain.

In the following we discuss this enlargement with respect to adaptive increases of brain component size ('encephalization'). Theoretically, the enlargement that we found could also be due to adaptive decrease in body size without a corresponding decrease in brain size ('somatization'). The latter can occur in secondary dwarfism, e.g. in talapoin monkeys *Miopithecus talapoin* [Stephan et al., 1988]. Somatization can also occur through an adaptive increase in body size [Towe and Mann, 1995]. Towe and Mann investigated two populations of Botta's pocket go-

pher (*Thomomys bottae*), which had adapted to habitats with different food supply, and observed a selection towards larger body sizes only. While it is possible, we think it is unlikely that somatization has occurred in any of our four study species.

The mesopallium of NC crows is significantly larger than that of the three other passeriformes we studied. This finding is consistent with previous work showing that mesopallial size predicts innovative and flexible behavior generally in birds [Timmermanns et al., 2000; Lefebvre et al., 2002, 2004]. The mesopallium as a whole is a true associative forebrain area that is not reached by any direct sensory pathway. Its ventral part includes critical areas for vocalization learning in songbirds, parrots and hummingbirds [Jarvis and Mello, 2000]. Partly overlapping with these, the anteroventral mesopallium contains a critical area for fast multimodal associative learning in the context of imprinting and avoidance learning [Rose, 2000; Horn, 2004]. A recent theory suggests that the mesopallium is also part of a circuit that controls sequencing and learning of motor actions [Feenders et al., 2008]. Thus, the mesopallium is involved in diverse associative functions and the production of learned complex motor sequences. The relative growth of this structure in NC crows makes it likely that the mental processes associated with the ability to manufacture and use tools are coupled with demands on multimodal forebrain systems.

NC crows had higher striatopallidal volumes than the other three passeriform species. Different pallial entities project into the avian striatum in a manner that parallels the mammalian brain, particularly neopallial regions such as the isocortex; for the comparability of avian and mammalian brain areas we refer to Kuhlenbeck [1967–1978], Rehkämper and Zilles [1991]; Rehkämper [1997]; Nieuwenhuys et al. [1998] and Reiner et al. [2004]. From here direct and indirect paths are sent back as loops to the pallium via a pallidothalamic pathway [Reiner, 2002]. This system was previously thought to be a mere motor pathway in primates, but is now known to primarily subserve action selection in the scope of various cognitive functions like categorization [Ashby et al., 2007], habit learning [Wickens et al., 2007] and context acquisition [Seeger, 2008]. Cortical and striatal neurons form tight loops that change their firing rates in a correlated manner during the acquisition of various sensorimotor learning tasks [Brasted and Wise, 2004]. To enable these learning-related changes in firing patterns, the projection of the ascending dopaminergic system is essential, which delivers a fast feedback about the outcome of an animal's own executed behavior. The organization of the dopaminergic projection into the striatopallidal and the pallial system is highly similar in mammals and birds [Durstewitz et al., 1999], and the striatopallidal complex is equivalent to that of the mammalian brain [Reiner et al., 2004]. These similarities between birds and mammals makes it likely that the relative increase of this complex in NC crows is associated with the cognitive and motor abilities of these birds to manufacture and apply tools to various known and novel problems.

The nidopallium of NC crows is enlarged as well, but this difference is not significant. However, the enlargement is consistent with the previously reported larger nidopallium size in true tool users [Timmermanns et al., 2000]. Particularly with its associative caudolateral part (neostriatum caudolaterale), which is thought to be a functional equivalent of the mammalian prefrontal cortex [Divac and Mogenson, 1985; Güntürkün, 2005], a relative increase of nidopallium volume suggests that this structure is part of the neural machinery required for cognitive skills associated with tool use. That the mesopallium rather than the nidopallium was significantly enlarged invites obvious speculation as to the contribution of these structures to tool skills. That is, the nidopallium may have more to do with the cognitive and motor skills required for basic tool use, while an enlarged mesopallium may be required for the enhancement of basic tool skills.

The relative increase of the tegmentum and the septum is interesting. The tegmentum bears structures that serve motor control [Nieuwenhuys et al., 1998] and therefore may be involved in the fine motor skills necessary for NC crows' tool manufacture and use. However, the tegmentum is not exclusively somatomotoric but also has many sensory nuclei and vegetative control centers [Nieuwenhuys et al., 1998].

The septum may integrate a variety of stimuli for the purpose of modulating complex behavior in a temporally, spatially and socially appropriate manner, probably in cooperation with the hippocampus [Goodson et al., 2004]. However, it also has non-associative functions and the fact that the NC crow's hippocampus is not enlarged might indicate that the septal enlargement is not linked to tool use and related cognitive behavior. Thus, the heuristic value of the coincidence of the increase of these structures with observed superior cognitive skills in NC crows is limited.

The comparison of the NC crow with carrion crow indicates that the enlargement of the associative areas that we found is not due to an evolved characteristic of the genus *Corvus* associated with highly flexible generalist foraging behavior.

Tool Manufacture and the Evolution of Cognition

Tool use per se is not an indicator of cognitive ability as a wide range of animals, including invertebrates, are reported to display tool use [Beck, 1980; Hansell, 2007]. However, the underlying mechanisms responsible for the evolution of a tool using lifestyle are probably very different across animals [van Lawick-Goodall, 1970]. Evidence suggests that the mechanisms in primates and birds are closely associated with cognitive flexibility [Timmermanns et al., 2000; Lefebvre et al., 2002; Reader and Laland, 2002; Emery and Clayton, 2004; Lefebvre et al., 2004; Hunt, 2005], while those in animal groups like invertebrates are rather rigid non-cognitive ones like those for construction behavior generally in these species [Hansell, 2005, 2007]. Although NC crows do not always attend to the functional properties of the tools that they routinely use [Holzhaider et al., 2008], they use causal knowledge rather than associative learning to solve complex physical problems [Taylor et al., 2007, 2009], individually specialize for certain tools [Hunt and Gray, 2007] and have at least a rudimentary grasp of the physical properties of the objects they work on [Weir et al., 2002]. These observations indicate that tool manufacture and use in NC crows is not part of a rigid motor program, but comes from a flexible cognitive ability that makes these

birds the most proficient non-human tool manufacturers. The increase of associative motor-learning-related areas that we found probably constitutes the neural basis for this cognitive ability. This finding conflicts with the recent suggestion that tool behavior in non-humans does not require special cognition but is rare simply because it is seldom useful [Hansell and Ruxton, 2008].

Our findings on the sizes of brain structures in NC crows support the hypothesis of a similar evolution of avian and mammalian brains [Karten, 1969; Rehkämper et al., 1991; Emery and Clayton, 2004; Güntürkün, 2005]. We found that the mesopallium (a true associative pallial area) as well as the striatopallidal complex are relatively enlarged in NC crows. This is also the case for primates that display proportionally enlarged associative forebrain areas and striatal volumes compared to other mammals [Stephan et al., 1988; Rehkämper et al., 1991; Keverne et al., 1996; Barton and Harvey, 2000; Sol et al., 2008]. Indeed, Stephan et al. [1988] was among the first to argue that the enlargement of the isocortex seen in apes and man is not due to primary regions like visual, auditory or somatosensory cortices, but to the non-primary areas including the association cortex.

The evolution of corvid and primate cognition and brain size has not been built on a similar evolution of the detailed architecture of their forebrains. While mammals

have a laminar arrangement of their pallium thus forming a cortex, the avian pallium displays a nuclear arrangement with a layering restricted to relatively small areas [Rehkämper et al., 1984; Ebinger et al., 1992; Jarvis et al., 2005]. Thus, cognition in corvids and primates evolved similarly with respect to mental capabilities, despite building on a different system of microcircuits [Güntürkün, 2005]. Our data, then, reveal an important additional principle of the evolution of cognitive functions: despite a different internal microstructure, an evolutionary increase of cognitive skills goes along with a volume increase of associative forebrain structures [Rehkämper et al., 1991]. In other words, enlargement of associative forebrain structures seems to be the default option in the evolution of cognitive skills.

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