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The Comparative Approach and Brain–Behaviour Relationships: A Tool for Understanding Tool Use

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The comparative method is widely used to understand brain–behaviour relationships in comparative psychology. Such studies have demonstrated functional relationships between the brain and behaviour as well as how the brain and behaviour evolve in concert with one another. Here, the authors illustrate with their data on tool use and cerebellar morphology in birds that such comparisons can be further extended to (a) relate the morphology of a brain region to a behaviour, and (b) provide insight into the function of an often overlooked brain region in comparative cognitive studies, the cerebellum. Their results indicate that tool-using species have a significantly more folded cerebellar cortex, but not a larger cerebellum than non-tool-using species. This marks the first demonstration of an empirical relationship between the folding of a neural structure and a cognitive behaviour and in so doing, provides critical insight into the neural basis of tool use and the role of the cerebellum in cognitive processes.

Keywords: tool use, cerebellum, comparative method, evolution, birds

The Snark Is No Longer a Boojum

In 1950, Frank Beach published a classic article entitled “The Snark Was a Boojum” in which he questioned the trend in comparative psychology to focus all of its attentions on the white lab rat (*Rattus norvegicus*). The question itself arose from Lewis Carroll’s nonsense poem “The Hunting of the Snark,” in which a hunting party sails away to a far-off land to search for Snarks. The catch, however, is that Snarks can readily be confused with Boojums and catching a Boojum will result in the hunter quickly and quietly disappearing. Beach likened the actions of the comparative psychologist to that of the hunters: The narrow focus on the lab rat would result in the disappearance of truly comparative psychology.

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Since the publication of Beach’s (1950) article, several retrospective and reviews have been published, all of which have questioned whether the Snark is a Boojum in relation to the general field of comparative psychology (Adkins-Regan, 1990; Dewsbury, 1998; Gosling, 2001; Hodos & Campbell, 1969). All of these publications, and many others, agree that comparative psychology today is truly comparative. In fact, a cursory examination of the species studied over the past 10 years in the *Journal of Comparative Psychology* reveals a wide array of species, including invertebrates, fish, amphibians, birds, and dozens of mammal species (see Figure 1). Comparative psychology, in its broadest sense, now even includes multispecies data sets in which attempts are made to understand the evolution of specific behaviours and the correlated evolution of the brain and behaviour. The latter studies, comparative studies of brain–behaviour relationships, have flourished in recent years as a result of increased interest in understanding how the brain has evolved (Striedter, 2005) as well as the development of advanced statistical methods to explore evolutionary patterns (Felsenstein, 1985; Garland, Dickerman, Janis, & Jones, 1993; Harvey & Pagel, 1991; Maddison & Maddison, 2003; Pagel, 1994). These studies range in scope from analyses of relative brain size in relation to various life history variables and behaviours (e.g., Iwaniuk, 2001, 2004; Perez-Barberia, Schultz, & Dunbar, 2007; Sol, Bacher, Reader, & Lefebvre, 2008; Sol, Szekely, Liker, & Lefebvre, 2007) to the size of brain regions in relation to specific behaviours (e.g., Barton, 1996; Iwaniuk, Clayton, & Wylie, 2006; Iwaniuk, Hurd, & Wylie, 2007; Iwaniuk & Wylie, 2006, 2007; Lindenfors, Nunn, & Barton, 2007; Pellis & Iwaniuk, 2002; review in Sherry, 2006). Despite the vast number of these

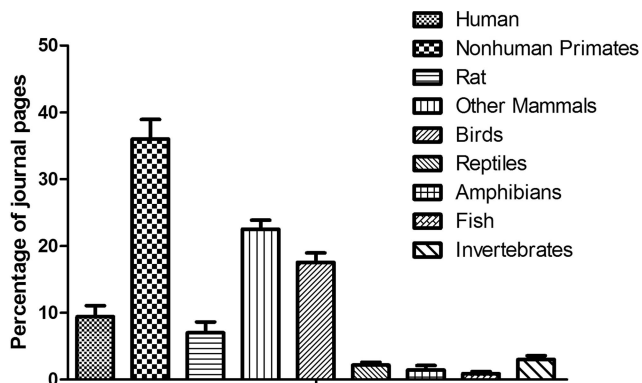


Figure 1. A bar graph of the percentage of pages per year (mean \pm standard deviation) devoted to each category of species in the *Journal of Comparative Psychology* from 1998 to 2008. Note that within all categories, except for "Human" and "Rat," the categories represent from several up to dozens of species.

studies in the literature, such comparative analyses of brain and behaviour are limited by the availability of suitable behavioural and neural data.

An inherent assumption of the correlational approach to brain-behaviour relationships is that selection for an enhanced cognitive ability should be accompanied by selection for improved efficiency of its neural substrate (Jerison, 1973), usually in the form of more neurons, which leads to an increase in neural structure size (Herculano-Houzel, Collins, Wong, & Kaas, 2007; Herculano-Houzel, Mota, & Lent, 2006). In some instances, the behaviour is readily assayable. For example, in the now classic comparisons of hippocampal volume and spatial memory in birds (see review in Sherry, 2006), spatial memory of the species or individuals can be readily tested and quantified through tasks such as food caching. Similarly, song complexity in songbirds can be quantified by counting the number of syllables and song types of an individual or species and related to the size of the vocal control nuclei (Ball & MacDougall-Shackleton, 2001; Garamszegi & Eens, 2004; Szekely, Catchpole, DeVoogd, Marchi, & DeVoogd, 1996). Most behaviours of interest to comparative psychologists or neuroscientists, however, reflect more generalised aspects of cognition, which are inherently difficult to test for adequately across species. Advances in estimating the cognitive capacity of different animal species have only recently made such comparisons possible, and they depend on obtaining a large amount of behavioural data (Deaner, Isler, Burkhart, & van Schaik, 2007; Deaner, van Schaik, & Johnson, 2006). An alternative to this approach is one adopted by Lefebvre and colleagues, which is to identify a cognitively based behaviour and mine the literature for any and all mentions of the behaviour. The result of this literature-based approach is an index of the capacity of a given species to perform the behaviour. One such behaviour that Lefebvre and colleagues have focused on is feeding innovations, which can be defined as previously unobserved or unknown behaviours that are produced during feeding. By examining all ornithological journals going back to 1930, they compiled a data set of all instances of novel feeding behaviours and birds and scaled this relative to the number of studies published on each species to yield an innovation rate: the number of

instances of novel feeding behaviours relative to the number of studies published on each species (reviewed in Lefebvre, Reader, & Sol, 2004). This index was subsequently used for several studies aimed at determining the neurological (Lefebvre, Gaxiola, Dawson, Rozsa, & Kabai, 1998; Lefebvre, Whittle, Lascaris, & Finkelstein, 1997; Timmermans, Lefebvre, Boire, & Basu, 2000) basis for species differences in innovation rate. The same approach was subsequently applied to avian tool use (Lefebvre, Nicolakakis, & Boire, 2002) and kleptoparasitism (Morand-Ferron, Sol, & Lefebvre, 2007) and to innovation, tool use, and social learning in primates (Reader & Laland, 2002).

Even with these advances in estimating the behavioural flexibility or cognitive capacity of species, relating the behaviour to the brain is constrained by a lack of suitable neural data. Studies of mammals rely heavily on the impressive data sets amassed by Heinz Stephan and colleagues for primates, bats, and "insectivores" (Baron, Stephan, & Frahm, 1996; Stephan, Baron, & Frahm, 1991; Stephan, Frahm, & Baron, 1981). For studies of other animals, however, data are scarce, and most researchers develop their own data sets or use the limited amount of information that is available. Over the past 8 years, we have initiated the development of a broad data set for birds (Iwaniuk, Heesy, Hall, & Wylie, 2008; Iwaniuk & Hurd, 2005; Iwaniuk, Hurd, & Wylie, 2005, 2006, 2007; Iwaniuk & Wylie, 2006, 2007). The results of these studies have yielded several significant findings in understanding how the avian brain evolves and how it relates to behaviour. For example, hummingbirds have significantly enlarged a region in the pretectum that responds to optic flow stimuli (see Figure 2a), which plays an important role in guiding hovering flight (Iwaniuk & Wylie, 2007). Similarly, owls, and a few other species, have significantly expanded the Wulst (see Figure 2b), which likely provides an advantage in binocular vision (Iwaniuk et al., 2008). Thus, it is possible to relate the size of brain regions other than the neocortex, hippocampus, and song system to behaviour, provided that suitable neural data can be obtained or generated.

Tool Use in Humans and Animals

There are many behaviours that comparative psychologists consider to be cognitively based, but one that has received increasing attention in recent years is tool use. The use of tools was once considered the exclusive domain of humans. Tool use is now recognised in all of the great apes (Breuer, Ndoundou-Hockemba, & Fishlock, 2005; Lohnsdorf, 2005; van Schaik, Fox, & Fechtman, 2003), other primates (van Schaik, Deaner, & Merrill, 1999), elephants (Hart, Hart, McCoy, & Sarath, 2001), and various birds including parrots (Borsari & Ottoni, 2005), corvids (Hunt, 1996), herons (Higuchi, 1986), and raptors (Ellis & Brunson, 1993). The corvids have gained much attention in this regard, with several studies illustrating the remarkable ability of New Caledonian crows (*Corvus moneduloides*) to use and manufacture tools to extract grubs from deep within wood (Hunt, 1996; Hunt & Gray, 2003, 2004) and, in the laboratory, to select and manufacture appropriate probes to extract food reward (Chappell & Kacelnik, 2002, 2004; Kenward, Weir, Rutz, & Kacelnik, 2005; Weir, 2002).

The evolution of tool use in all of the taxa listed above is correlated with significant changes in the relative size and composition of the brain. In hominids and other primates, species that

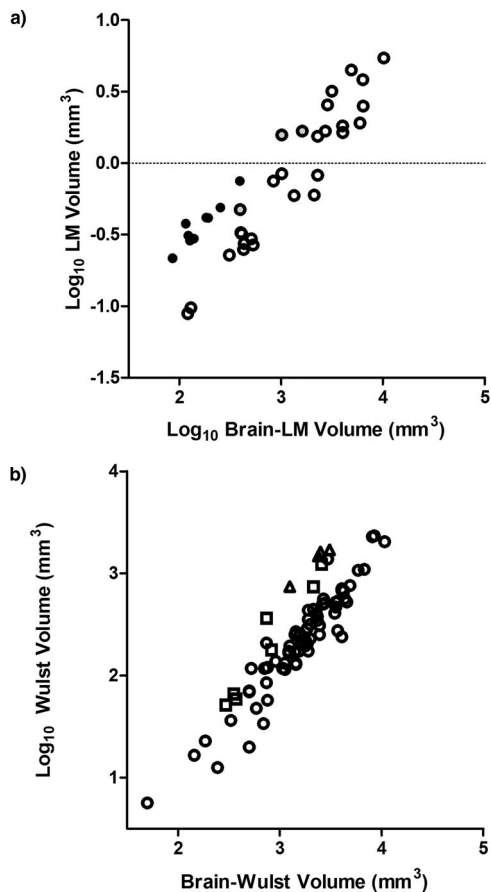


Figure 2. (a). A scatterplot of the volume of the nucleus lentiformis mesencephali against brain volume in 37 species of birds. Black circles indicate hummingbirds (Trochilidae), grey circles indicate three species classified as transient hoverers (belted kingfisher [*Ceryle alcyon*], Eastern spinebill [*Acanthorhynchus tenuirostris*], and American kestrel [*Falco americanus*]), and the white circles are all other species examined (for details, see Iwaniuk & Wylie, 2007). (b). A scatterplot of the volume of the Wulst against brain volume in 76 species of birds. The triangles represent the owls (Strigiformes), the squares represent members of the Caprimulgiformes (nightjars and allies), and the circles represent all other species (for details, see Iwaniuk & Wylie, 2006).

use tools more frequently have relatively larger brains and neocortical volumes than species that rarely or never use tools (Gibson, 2002; Reader & Laland, 2002; Weaver, 2005) and a similar correlation is present in birds (Lefebvre et al., 2002). Together, this comparative evidence indicates that there is a general evolutionary trend whereby tool use is correlated with increases in relative brain and forebrain size, but is there a role for other brain regions?

The cerebellum is one such structure that is likely involved in tool use. Evidence for the role of the cerebellum in tool use is provided by several studies in monkeys and humans that demonstrate increased cerebellar activity during tool use (Imamizu, Kuroda, Miyauchi, Yoshioka, & Kawato, 2003; Obayashi et al., 2001; Tamada, Miyauchi, Imamizu, Yoshioka, & Kawato, 1999). Cerebellar expansion also coincides with the development of stone tool production and increasing cultural complexity in human evolution (Weaver, 2005). In addition, the cerebellum is traditionally

thought of as a key centre for motor control and learning (Ito, 1984; Thach, 1998), and the successful use of tools relies heavily on motor learning (Lohnsdorf, 2005; Tebbich, Taborsky, Fessl, & Blomqvist, 2001). Tool use also involves precise integration of visual and tactile signals coming from the implements being manipulated and the cerebellum is active in sensory integration (Arends, 1997; Bower, 1997). The cerebellum is also critical for cognitive processing (Day, Westcott, & Olster, 2005; Paulin, 1993; Thach, 1998; Rodríguez et al., 2005), and tool use is considered to be a cognitively demanding behaviour (Lefebvre et al., 2002; Parker & Gibson, 1977; Tebbich & Bshary, 2004). Thus, multiple lines of evidence suggest that the cerebellum might play a role in the evolution of tool use.

Previous analyses have demonstrated that there is no correlation between cerebellar volume and tool use (Lefebvre et al., 2002; Reader & Laland, 2002), but there is more to the cerebellum than just its size. Despite the conservative cellular organisation of the vertebrate cerebellum (Voogd & Glickstein, 1998), there is significant variation in its overall morphology. The cerebellum of most vertebrates consists of a singular thin sheet overlaying the hind-brain. In birds and mammals, the cerebellar cortex is not only enlarged, but has also become a complex folded structure consisting of numerous lobules or folia (Larsell, 1967, 1970). In fact, one of the major differences among birds and mammals is the degree of folding or foliation of the cerebellum. For laminated structures, such as cerebellar and cerebral cortices, length is thought to reflect processing demands in a similar fashion to the volume of other structures (Striedter, 2005; Sultan, 2002, 2005). The primary means of increasing the relative length of a folded structure such as the cerebellum is to increase the degree of foliation of the structure (Striedter, 2005). Thus, if the evolution of tool use is correlated with relative cerebellar cortex length, then species that use tools more frequently should possess more foliated cerebella than species that rarely or never use tools. A comparative test of foliation in a wide range of species would also go a step beyond the current emphasis on simple volume of neural structures, which some (e.g., Roth & Dicke, 2005) argue to be less informative than other neuroanatomical measures. In a recent study, we compared the degree of foliation of the cerebellum of birds spanning a large number of taxa (Iwaniuk et al., 2005, 2007; Iwaniuk, Hurd, & Wylie, 2006). We found that the degree of cerebellar foliation was most pronounced in birds that are traditionally regarded as “smart”: parrots, corvids, and gulls. However, a direct correlation between a cognitive measure and cerebellar foliation would be useful. Here, we provide evidence that cerebellar foliation and tool use are evolutionarily correlated using our broad database on cerebellar size and morphology of birds (Iwaniuk et al., 2005, 2007; Iwaniuk, Hurd, & Wylie, 2006).

Testing the Relationship Between Tool Use and the Cerebellum

In a recent series of studies, we documented species differences in cerebellar size and morphology, including the relative size of individual folia and the overall degree of folding, or foliation, of the cerebellum (Iwaniuk et al., 2005, 2007; Iwaniuk, Hurd, & Wylie, 2006). Overall, the greatest amount of variation in cerebellar morphology is the degree of foliation; therefore, we examined this measurement, in addition to cerebellar volume, in light of tool

use. Briefly, foliation is calculated by measuring the total length of the Purkinje cell layer divided by the length of the envelope, which follows the dorsal surface of the Purkinje cell layer without counting the depth of the folia (Figure 3a). Details for all of the foliation measurements and cerebellar volumes are provided in Iwaniuk, Hurd, and Wylie (2006).

The tool use data set consists of 126 cases in 107 species (125 from the review by Lefebvre et al., 2002, plus the only new case of tool use in birds published since, Borsari & Ottoni, 2005). Because reports of tool use are likely to be more frequent in well-studied species, we used residuals of log frequency of tool use or feeding innovation regressed against log research effort, which was measured by the number of publications listed for each species in the 1978–2005 online versions of the *Zoological Record*. For tool use, we used only cases involving feeding and drinking, following Lefebvre et al. (2002). Following the tradition in the literature (e.g., Beck, 1980), we separate tools into two categories thought to differ in cognitive and motor complexity: *true tools* ($n = 40$), where an external implement is held in the foot or beak, and *borderline* or *prototools* ($n = 86$), where an animal acts on food by using an environmental feature that it does not hold. According to this distinction, an Egyptian vulture (*Neophron percnopterus*) that breaks an ostrich egg with a rock held in its beak uses a true tool, whereas a gull (*Larus* sp.) that drops a shell on a rock uses a prototool. Because the integration of motor and cognitive skills is thought to be more complex in true tool use, we predicted that cerebellar foliation will be more closely correlated with true tools than with prototools.

As with the size of the brain as a whole or any brain region (Harvey & Pagel, 1991), cerebellar (Cb) volume scales positively with body and brain size. We therefore size-corrected Cb volume by calculating residuals from a least squares linear regression of log Cb volume against log brain volume minus Cb volume (Deacon, 1990). Previous reports have suggested that the degree of cerebellar foliation is correlated with body and brain size (Pearson & Pearson, 1976; Senglaub, 1963). We found significant correlations between the cerebellar foliation index (CFI) and log body mass, log Cb volume, and log brain volume (all $ps < .01$). The residuals from the CFI–body mass regression were, however,

correlated with both Cb and brain volumes, which indicated that residuals from an individual regression line do not remove all allometric effects. To account for all allometric effects, we therefore performed a principal components analysis on three scaling variables: log body mass, log Cb volume, and log brain minus Cb volume (Iwaniuk, Hurd, & Wylie, 2006). The first principal component, which explained 95.5% of the variation in all three variables, was then used as the independent variable in a least squares linear regression with log CFI as the dependent variable. The residuals from this regression were used as a measure of relative CFI independent of allometric effects.

Previous analyses of feeding innovations and tool use in birds (Lefebvre et al., 1997, 1998, 2002) used averages of higher taxonomic levels to test for correlations because most of the taxonomic variation was present at high (e.g., order, family) rather than low (e.g., genera, species) levels. A nested analysis of variance indicated that variation at the level of Sibley and Ahlquist's (1990) parvorder/infracorder— $F(18, 9) = 17.46, p < .0001$ —also accounted for most of the variation in relative CFI compared to lower taxonomic levels (all $ps < .05$). We therefore conducted all of our analyses at the parvorder/infracorder level using least squares linear regression to test for significant relationships. For all comparisons, we performed least squares linear regressions to determine whether tool use and feeding innovations were significantly correlated with the neuroanatomical variables. Significant outliers were detected using Mahalanobis distance methods as implemented in JMPIN (SAS Institute).

Phylogenetic relationships among species can confound statistical tests because species are not truly independent data points (Harvey & Pagel, 1991; Iwaniuk, 2004; Iwaniuk, Pellis, & Whishaw, 1999). To account for these confounding effects of phylogeny, we calculated independent contrasts (Felsenstein, 1985) using PDTREE, a program within the PDAP software package (available from T. Garland on request). We used the phylogeny provided in Sibley and Ahlquist (1990) and performed diagnostic tests on all branch lengths to ensure that the data were adequately standardised (Garland, Harvey, & Ives, 1992). The independent contrasts regressions were forced through the origin (Garland et al., 1992).

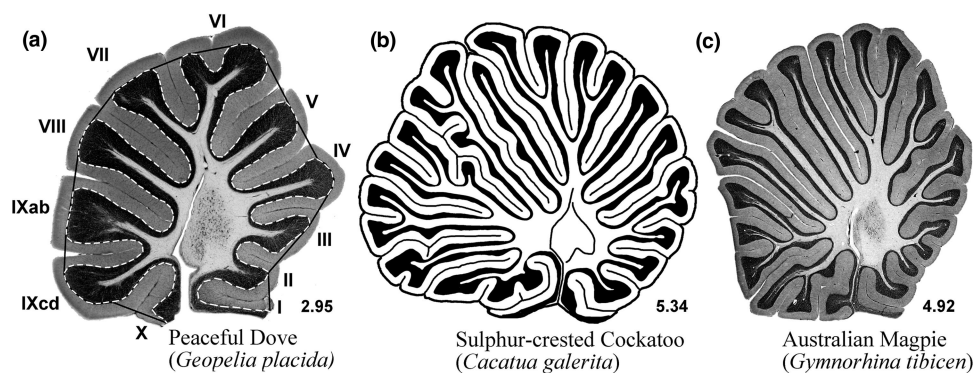


Figure 3. Midsagittal sections through the cerebellum are shown for three species: (a) peaceful dove (*Geopelia placida*), (b) sulphur-crested cockatoo (*Cacatua galerita*), and (c) Australian magpie (*Gymnorhina tibicen*). The numbers represent the cerebellar foliation index (CFI) calculated for each species. The CFI was the ratio of the two measurements shown in (a): the dotted white line, which is the outline of the Purkinje cell layer, and the solid black line, which is the envelope of the cerebellar cortex.

Cerebellar Function From a Comparative Perspective

Our CFI varies significantly among taxa. At one end of the spectrum, both parrots and corvids had high relative CFIs (see Figures 3 and 4a). Pigeons (Columbiformes), waterfowl (Anseriformes), and rails (Ralli), on the other hand, had relatively low CFIs (see Figure 4a). This variation in relative CFI was not, however, concordant with relative cerebellar volume, $t(18) = 0.89$, $p = .39$. For example, parrots have relatively high CFIs, but relatively low Cb volumes (see Figure 4). Thus, a relatively highly foliated cerebellum does not necessarily indicate a relatively large cerebellum.

As predicted, relative CFI was positively correlated with true tool use (see Figure 5a). This was corroborated by independent contrast analyses (see Figure 5b) and is therefore not due to the confounding effects of phylogeny. True tool use was not significantly related to relative Cb volume, either with (see Figure 5c) or without (see Figure 5d) independent contrasts. The use of proto-tools was not significantly associated with either CFI (see Figures 6a and 6b) or relative Cb volume (see Figures 6c and 6d). These results agree with our observations of interspecific variation in both CFI and tool use. For example, corvids and parrots have relatively high CFIs, low Cb volumes, and high true tool use rates. In contrast, pigeons and chicken-like birds (Phasianida) have relatively low CFIs, moderate Cb volumes, and no tool use. Thus, true tool use and relative CFI are evolutionarily correlated.

Unlike most previous comparative studies that only examined the relative size of a brain region (Barton, 1996; Iwaniuk, Clayton, & Wylie, 2006; Iwaniuk et al., 2007; Iwaniuk & Wylie, 2007; Lindenfors et al., 2007; Pellis & Iwaniuk, 2002), we show that true

tool use in birds is correlated with a shape metric, the relative degree of cerebellar foliation, and not the relative volume of the cerebellum itself. Folding of laminated structures is thought to increase the processing capacity of a structure (Striedter, 2005; Sultan, 2002). Indeed, from the time of Erasistratus (third century B.C.), it has been postulated that the degree of folding in neural structures might be correlated with behaviour or cognitive abilities (Finger, 2000; Striedter, 2005). Despite this long-held belief, empirical evidence to support such a correlation has been lacking. Farris (2008; Farris & Roberts, 2005) has recently shown that the degree of folding of mushroom bodies in insects is associated with differences in diet breadth, but our study is the first to show that the folding of a neural structure is associated with a specific cognitive ability: tool use.

Folding results in a larger surface area without necessarily affecting volume (Striedter, 2005), and this was observed in our data set; some taxa have relatively high CFIs but relatively small Cb volumes, and vice versa. Increasing the degree of foliation without affecting Cb volume may be a means of responding to increased processing demands on the cerebellum (Sultan, 2002, 2005). If true, then there are several reasons why true tool use may have placed higher motor, sensory, and cognitive processing demands on the cerebellum.

Although tool use can develop spontaneously during ontogeny, some degree of practise and learning is required for tool use to be effective. For example, woodpecker finches (*Cactospiza pallida*) will use tools without previous experience, but their proficiency in using these tools is improved by repeated use and practise (Tebich et al., 2001). Furthermore, the development of tool use in

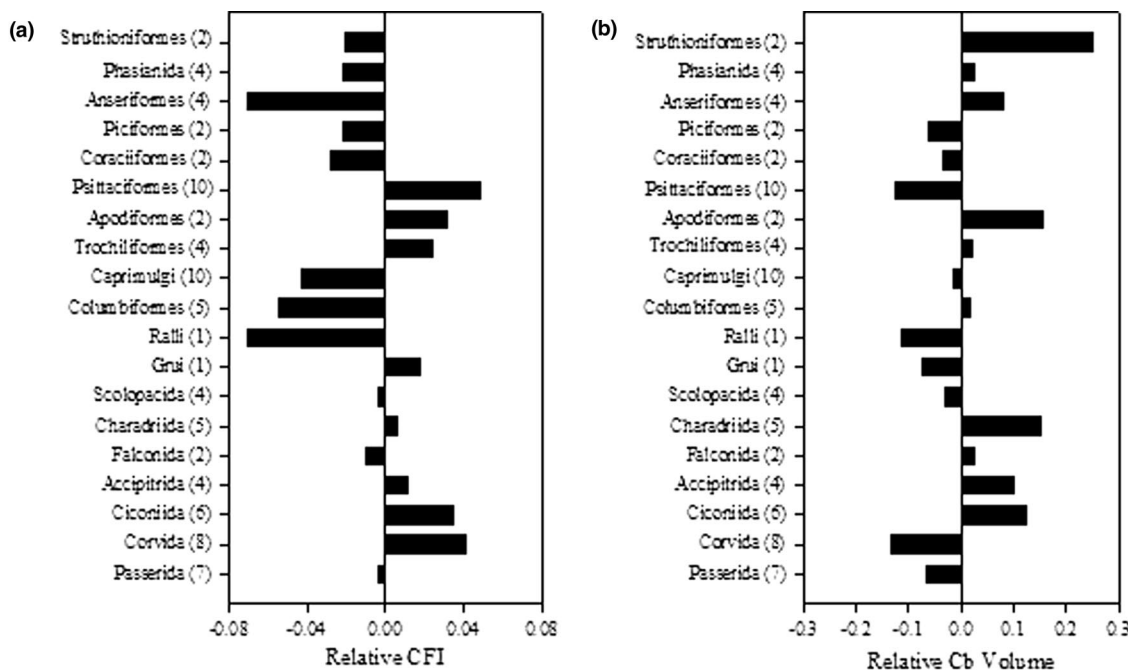


Figure 4. Bar graphs indicating the variation in (a) relative cerebellar foliation index (CFI) and (b) cerebellar (Cb) volume among the parvorders surveyed. The parvorders are organised as they appear in Sibley and Ahlquist (1990) and reflect a progression from basal to distal tips of the avian phylogeny. The number of species surveyed within each parvorder/infracorder is provided in parentheses.

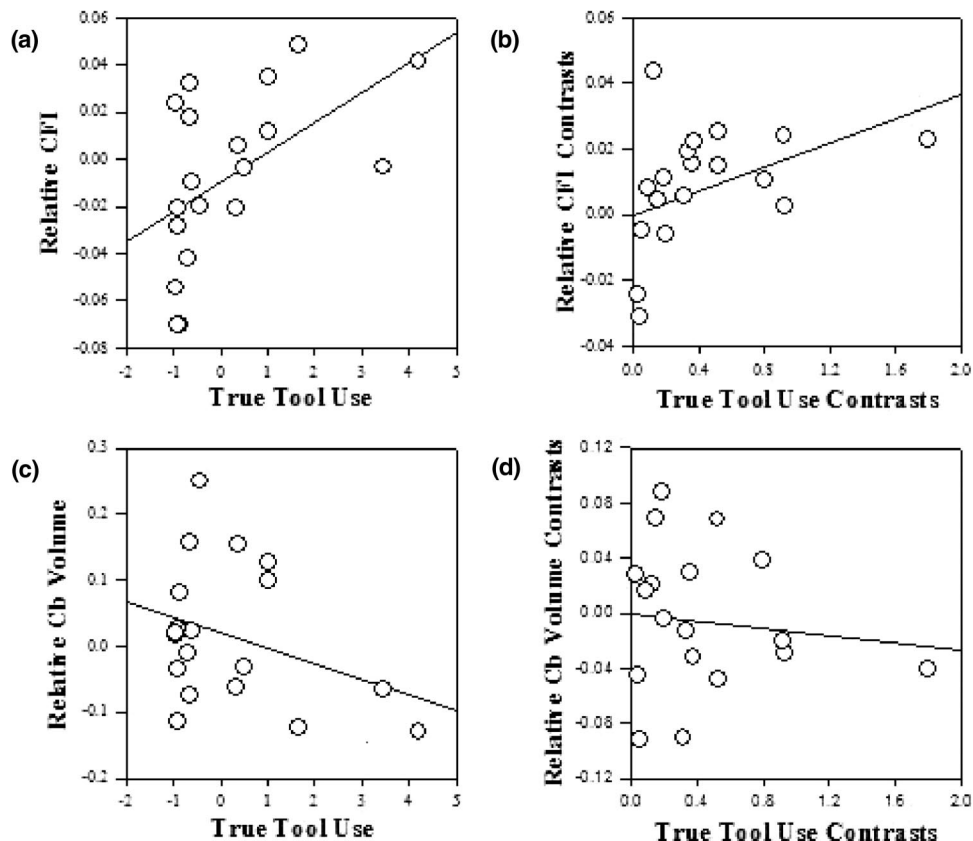


Figure 5. Scatterplots of (a) relative cerebellar foliation index (CFI) against true tool use ($r^2 = .24$); (b) relative CFI contrasts against true tool use contrasts ($r^2 = .14$); (c) relative cerebellar (Cb) volume against true tool use ($p < .10$); and (d) relative Cb volume contrasts against true tool use contrasts ($p < .10$). The solid lines represent the least squares linear regression lines.

this species is characterised by the sequential addition of new behaviours until the final tool use repertoire is achieved. A similar effect of motor learning on tool proficiency occurs in other species as well (e.g., Lohnsdorf, 2005). As mentioned previously, the “traditional” view of the cerebellum is that it is involved in movement coordination and motor learning, and there is ample evidence to support this claim (Ito, 1984; Thach, 1998). An increase in the amount of motor processing or motor learning brought about by tool use could therefore have placed increased processing demands on the cerebellum.

Tool use is not only dependent on motor learning, it also involves the coordination of visual and somatosensory information. This is best illustrated by the use of probing tools in birds. The probe is held in the beak and is moved around inside crevices using precise and subtle movements to force out prey items (Kenward et al., 2005; Tebbich et al., 2001). To accomplish this, the bird must coordinate tactile and visual information in such a way that the movements are precise enough to extract the food item. In addition to motor control, the cerebellum is also involved in the acquisition of sensory information (Bower, 1997). Given this role and the fact that the avian cerebellum receives projections from multiple sensory modalities (Arends, 1997), an increased reliance on sensory integration during tool use could also place increased processing demands on the cerebellum. Effective tool use also requires an

exquisite timing of the subtle movements involved. In recent years, it has been suggested that the cerebellum acts as a timing device and is critical for generating temporal rhythms (e.g., Thach, 2007; Yarom & Cohen, 2002). Thus, the requirement of precise timing during tool use also may have increased processing demands on the cerebellum.

Because of its reliance on learning as well as the integration of sensory information, tool use is generally considered to be a cognitively demanding behaviour. By its very nature, tool use involves the causal relation of two (or more) objects external to the animal’s body (Parker & Gibson, 1977). Experiments in woodpecker finches have shown that tool use can be modified to suit specific circumstances and is refined by trial and error learning (Tebich & Bshary, 2004). Similarly, New Caledonian crows select tools that are appropriate for the task (Chappell & Kacelnik, 2002, 2004), which suggests advanced cognitive abilities. These crows are also able to pass the trap tube test (Taylor, Hunt, Medina, & Gray, 2009), which requires a flexible use of tools depending on the causal relationship between the crow, food, and trap such that access to the reward occurs only if the tool is properly used. The cerebellum is still predominantly considered a motor or sensorimotor structure, but recent studies suggest that it may play a significant role in cognitive processing as well (Day et al., 2005; Paulin, 1993; Rodríguez et al., 2005; Thach, 1998),

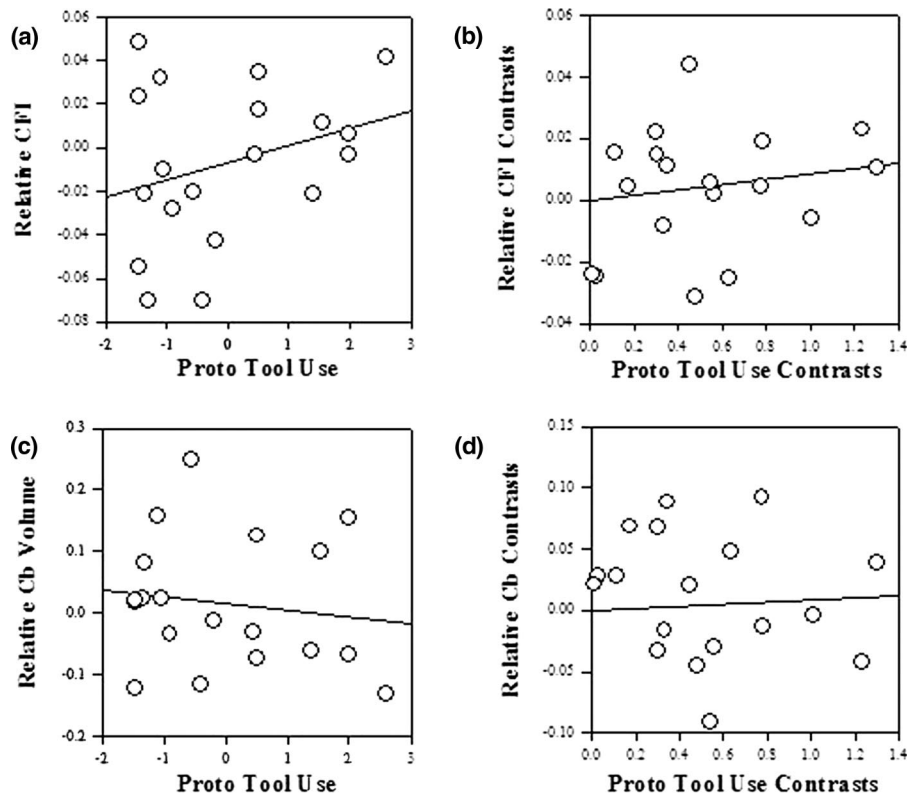


Figure 6. Scatterplots of (a) relative cerebellar foliation index (CFI) against prototool use ($p < .10$); (b) relative CFI contrasts against prototool use contrasts ($p < .10$); (c) relative cerebellar (Cb) volume against prototool use ($p < .10$); and (d) relative Cb volume contrasts against prototool use contrasts ($p < .10$). The solid lines represent the least squares linear regression lines.

although the details of its contribution remain unclear (Bower, 1997; Paulin, 1993; Thach, 1998). Our finding that a behaviour considered to be one of the most cognitively demanding for nonhumans (Boesch, 1996) is associated with relative CFI is consistent with this recent reassessment of cerebellar function.

Together, the processing demands brought on by motor learning, somatosensory integration, and cognitive processes during tool use may be responsible for the observed correlation between tool use and cerebellar foliation. These demands appear to be greater for true tool use than they are for prototools, as we detected a significant correlation only in the former case but not the latter. The main distinction between the two types of tools is that true tool use involves the fine manipulation of an implement, including more intricate movements and coordination of the eye and beak (e.g., use of probe tools). In contrast, the use of a prototool, such as a stone anvil to break open a snail, involves a much more repetitive and stereotyped series of movements. Birds that use true tools correspondingly have a relatively larger brain than birds that use prototools (Lefebvre et al., 2002).

Most of the birds that use tools do not manufacture them; instead, they use objects found in their environment (e.g., Ellis & Brunson, 1993; Higuchi, 1986). Corvids and parrots both exhibit relatively high values for true tool use, forebrain size, and CFI, and are the only taxa that have as yet been observed manufacturing tools. The hyacinth macaw (*Anodorhynchus hyacinthus*), a neotro-

pical parrot, makes wedges out of wooden perches to assist in opening *Indaia dubia* nuts (Attalea dubia; Borsari & Ottoni, 2005). Similarly, New Caledonian crows manufacture a variety of tools including hooks (Hunt, 1996; Hunt & Gray, 2004; Weir, 2002) and “step-tools” involving up to four ripped notches on *Pandanus* leaves, a technique possibly characterised by a cumulative technological evolution typical of culture (Hunt & Gray, 2003). The relatively high CFI of both parrots and corvids therefore may not only reflect their ability to use tools, but also the motor, sensory, and cognitive demands of tool manufacture.

Whether evolutionary changes in the cerebellar cortex of non-avian also coincide with changes in tool use or other behaviours remains to be shown. Humans have relatively small cerebella compared with other primates (Rilling & Insel, 1998), but both apes and humans have more folded cerebella than other primates (Larsell, 1970). Increasing the relative amount of folding in the cerebellar cortex, without significantly affecting its relative volume, may therefore be a common means of achieving proficient tool use that complements increases in relative forebrain size.

The Future of Comparative Brain–Behaviour Studies

Tool use is only one of many behaviours of interest to comparative psychologists, and the field is virtually wide open to investigate other behaviours. Again, the primary constraint on pursuing

such studies is the availability of suitable data. In terms of tool use, our analyses provide some insight into general patterns of cerebellar-tool use evolution across all birds, but whether it applies to more restricted comparisons, such as the New Caledonian crow compared with other corvids, remains to be tested because of a lack of suitable neural data. Similarly, the work of several labs on crows, jays, and their relatives is providing detailed information about species differences in social cognition (Bond, Kamil, & Balda, 2002, 2007; Bugnyar, Schwab, Schloegel, Kotschal, & Heinrich, 2007; Emery & Clayton, 2004; Schwab, Bugnyar, & Kotschal, 2008; Seed, Clayton, & Emery, 2008), but again, there is a lack of accompanying data on brain composition. With the rapid development of various imaging techniques for use in small animals (Corfield, Wild, Cowan, Parsons, & Kubke, 2008; Van der Linden, Van Camp, Ramos-Cabrer, & Hoehm, 2007), it may be possible to amass larger data sets on brain composition and morphology relatively quickly, which would enhance future studies of brain-behaviour relationships. In the meantime, it is quite clear that the “comparative” part of comparative psychology is alive and well and promises to continue to provide insight into general aspects of animal behaviour, including evolution.

Résumé

La méthode comparative est largement utilisée pour étudier les relations cerveau-comportement en psychologie comparative. Ces études ont démontré des relations fonctionnelles entre le cerveau et le comportement et fait ressortir la façon dont le cerveau et le comportement évoluent de concert l'un avec l'autre. Les auteurs illustrent ici avec leurs données sur l'utilisation d'outils et la morphologie cérébelleuse des oiseaux que de telles comparaisons peuvent aussi s'appliquer pour (a) lier la morphologie d'une région du cerveau au comportement et (b) fournir des pistes quant à la fonction d'une structure souvent négligée dans les études comparatives cognitives, le cervelet. Leurs résultats indiquent que le cortex cérébelleux des espèces utilisant des outils possède plus de circonvolutions, mais n'est pas plus gros que celui des espèces n'utilisant pas d'outils. Ceci constitue la première démonstration d'un lien empirique entre les circonvolutions d'une structure neurale et le comportement cognitif et fournit ainsi des pistes cruciales quant aux bases neurales de l'utilisation d'outils et au rôle du cervelet dans les processus cognitifs.

Mots-clés : utilisation d'outils, cervelet, méthode comparative, évolution, oiseaux

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