

Article

Brain Size Associated with Foot Preferences in Australian Parrots

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Abstract: Since foot preference of cockatoos and parrots to hold and manipulate food and other objects has been associated with better ability to perform certain tasks, we predicted that either strength or direction of foot preference would correlate with brain size. Our study of 25 psittacine species of Australia found that species with larger absolute brain mass have stronger foot preferences and that percent left-footedness is correlated positively with brain mass. In a sub-sample of 11 species, we found an association between foot preference and size of the nidopallial region of the telencephalon, an area equivalent to the mammalian cortex and including regions with executive function and other higher-level functions. Our analysis showed that percent left-foot use correlates positively and significantly with size of the nidopallium relative to the whole brain, but not with the relative size of the optic tecta. Psittacine species with stronger left-foot preferences have larger brains, with the nidopallium making up a greater proportion of those brains. Our results are the first to show an association between brain size and asymmetrical limb use by parrots and cockatoos. Our results support the hypothesis that limb preference enhances brain capacity and higher (nidopallial) functioning.

Keywords: parrots; footedness; brain mass; body mass; nidopallium; optic tectum; optic tecta; Wulst; lateral asymmetry



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1. Introduction

Hand and foot preferences (footedness) have often been used as proxy measures of brain lateralization although there is little evidence that these preferences correlate with structural differences in the brain [1]. In humans, however, non-right handedness has been associated with particular dysfunctional conditions, although not consistently [2–5]. In non-human species, absence of hand or limb preference has been considered to indicate weak or absent asymmetry of the brain [6,7]. However, although hand-preference, or limb-preference, reflects which hemisphere is in control of motor behaviour [8], its presence or absence cannot not necessarily be used as a measure of the strength or direction of asymmetry in the brain itself, either at the individual level or the population level. For example, in any group of marmosets, approximately half the individuals have a left-hand preference and the other half a right-hand preference [9]. Nevertheless, almost all individuals have the same eye preference for viewing particular stimuli [10]. Furthermore, left-handed marmosets have a negative cognitive bias, whereas right-handed marmosets have a positive cognitive bias [11]: a result explained by specialised processing of the hemisphere contralateral to the preferred hand. In marmosets, hand preference is an individual characteristic, whereas eye preference has a population bias. Even when no consistent limb preference is present, a species may still have population asymmetry for processing sensory information in the brain.

Some researchers adhere to the hypothesis that hand preference in humans is stronger than any hand or limb preference in non-human species [12]. By extrapolation, it has also been argued that brain lateralization is stronger in humans, thereby adhering to a view of a significant discontinuity of brain function between humans and other animals [13,14] but see [15]. Although there is some support for this idea when only the evidence for

hand preference in primates is considered, that too has been contested [14,16]. In fact, we now know that limb preferences present as population-level asymmetries are quite common in vertebrate species [12]. They occur in some amphibians [17,18], and footedness has been reported for several avian orders (wildfowl and waders [19], yellow-bellied tits, *Pardaliparus venustulus*, [20] and many species of parrots [21,22]). Cockatoos also display foot preferences [21,23–25] and, in some species, foot preference is as strong as hand preference in humans [21]. Furthermore, the well-studied laterality of a broad range of perceptual functions in chickens and pigeons is as strong as laterality in humans [26–29].

Having a lateralized brain has been shown to increase the processing capacity of the brain, to permit complementary and parallel processing of sensory information and to improve motor control [27]. Consistent with this, psittacine species that display foot preferences have better ability to perform certain tasks than species with weak or no foot preference [30,31]. This raises questions about potential associations between brain size and foot preference in different psittacine species. Do species with footedness have larger brains, or is footedness a way of compensating for having a smaller brain?

In this paper we are concerned with species-level population lateralization of foot use in a range of species of Australian parrots and cockatoos. Psittaciformes are usually subdivided into three superfamilies: Cacatuoidea (cockatoos), Psittacoidea (true parrots) and Strigopoidea [32]. Species in Strigopoidea were not included here because they are extant New Zealand parrots. Worldwide, there are about 375 species of parrots, of which about 56 species (depending on taxonomical consideration of counting some birds as subspecies or separate species) are native to Australia. Modern extant parrots and songbirds are of particular interest for evolutionary reasons [33]. Both orders have their origin in East-Gondwana, now Australia [34]. While radiations and departures from the continent eventually occurred, the evolution of the two superfamilies from ancestral surviving lineages has been uninterrupted to this day, despite the mass extinction events of 65 million years ago [33,35].

Large-brained psittacines, as cockatoos are, have a unique cerebrotypology compared to large-brained songbirds: they have a relatively larger subpallium within the telencephalon, containing more telencephalic neurons [36]. The subpallium is responsible for neural regulation of feeding, reproduction, voluntary movement, and agonistic and stress behaviours. It is also associated with reward, memory and learning [37].

Parrots are an anomaly amongst avian species in that their brains are lavishly equipped with nuclei for vocalizations, having the same seven nuclei of the song control system as songbirds, although they are not songbirds. Parrots are well-known for their extraordinary ability to mimic and to retain the memory of a large number of sounds that are not species-specific. Why this capacity has developed is not clear because it has so far not been confirmed that parrots use mimicry in the wild on a regular or even just occasional basis. Even more puzzling, from a functional point of view, is, as Chakraborty and colleagues [38,39] discovered, that parrots have a core and shell song systems, i.e., an additional set of nuclei not present in songbirds. It seems to be a structure unique to the parrot brain but its function is still not entirely clear. We now know, however, that within the song control system the magnocellular nucleus of the medial striatum (MMSt) is a prime target for somato-motor outputs from the hyperpallium apicale of the rostral Wulst, the avian equivalent of the mammalian motor cortex [40]. This projection may be significant in parrots as it potentially mediates control of the body and limbs along with vocalization during elaborate, ritualized visual displays [41]. One notes that the song nuclei are largely located in the nidopallium, the part of the forebrain that is involved in cognition.

We report associations between foot preference (footedness) in species of Australian parrots and brain size, measured as whole brain mass and as whole brain mass relative to body mass, and between footedness and the size of two regions of the brain, the nidopallium, including the primary visual centre (entopallium), and the optic tectum. The avian nidopallium (see Figure 1), an analogue to the mammalian cortex, is an important

area of the cortical telencephalon of the avian forebrain. Some of its sub-regions, such as the caudal nidopallium, the nidopallium caudocentral (NCC), caudomedial (NCM) and caudolateral (NCL), are considered vital for many complex, higher order cognitive functions in birds [42–44]. Indeed, the NCL is the seat of executive function, functionally equivalent to the prefrontal cortex of mammals [44,45] and, amongst other connections, it is reciprocally connected to sensory areas in all modalities and to basal ganglia and premotor areas [46]. It plays a key role in cognitive control of a number of functions, including roles in reward systems [47] and choice behaviour [48]. Although no studies of NCL have yet been conducted using parrots, this region of the nidopallium is almost certainly involved in feeding using the feet.

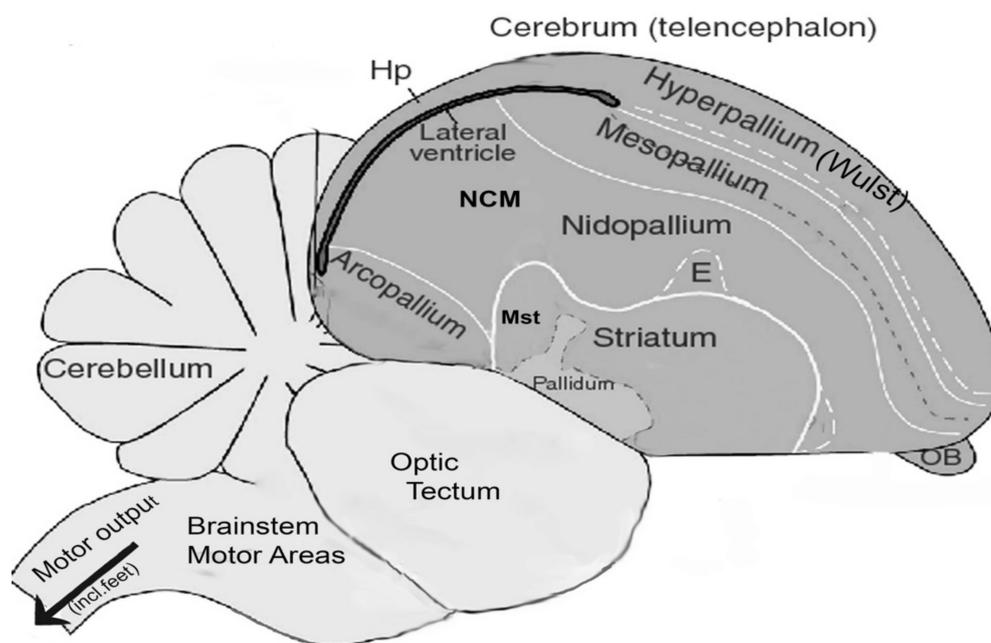


Figure 1. Brain regions of the parrot brain. Our text focusses on the Nidopallium and Optic tectum, as marked. Note that the optic tectum is located laterally on each side of the brain and in this Figure it obscures the midbrain and most of the hypothalamus. The darker section indicates the forebrain (telencephalon). Abbreviations: Hp = Hippocampus; NCM = Caudiomedial nidopallium; MSt = medial striatum; E = Entopallium; OB = Olfactory bulb. Adapted from Chakraborty and Jarvis [39], Kuenzel et al. [49] and Reiner et al. [50]. The Nidopallium includes NCM, E and Arcopallium, as well as other regions discussed in the text.

The optic tectum is part of the main visual input system of birds and must be involved in foot/eye coordination. However, Niederleitner et al. [51] discovered a relay nucleus between the inferior colliculus and the optic tectum in the chicken, providing a solid basis for demonstrating visual–auditory integration.

We were interested in testing whether limb preference might be associated with the size of these of the optic tectum and the nidopallium because eye preferences and foot preferences are linked, as Brown and Magat showed in 16 species of Australian parrots [52].

2. Materials and Methods

2.1. Subjects

Psittaciformes are subdivided into the superfamilies Strigopoidea (New Zealand parrots), Cacatuoidea (cockatoos) and Psittacoidea (true parrots). Species in our samples, which did not include the New Zealand parrots, belonged to the two superfamilies of cockatoos (Cacatuoidea) and true parrots (Psittacoidea). Those examined here are exclusively native Australian species, excluding closely related cockatoo species endemic to islands north of Australia (such as New Guinea, including the Bismarck Archipelago, the Solomon

Islands, or Tanimbar Islands Archipelago (Indonesia). The subjects used were those for which published data on brain mass, body mass and foot preference are available (see next section) but for which no previous study exists that has tested a potential association between these variables.

2.2. Source of Data

Data on body mass, brain mass and volumes of brain regions were obtained from Franklin et al. [53] and Iwaniuk et al. [54]. We compared published data on foot preferences (see below) with published data on brain mass, relative brain mass and the size of two regions of the forebrain, the nidopallium and the optic tectum.

Foot preference in 25 species of Australian parrots was obtained from three publications. Data for nine species were obtained from a previous study by the co-author of this paper, Rogers [21]. Scores for the budgerigar came from Rogers and Workman [55] and for another 15 species from Brown and Magat [22] (see Table 1). We used data for two measures of footedness: (1) percent use of the left foot and (2) strength of foot preference, regardless of whether the left or right foot is used.

Table 1. Psittacine species used. No = number of individuals scored, % Left = (Left/Left + Right) × 100, and the ratio of brain mass/body mass × 1000.

| Common Name | Latin Species Name | No | % Left | Strength | Brain Mass /Body Mass × 1000 |
|------------------------------|----------------------------------|----|--------|----------|------------------------------|
| Galah | <i>Eolophus roseicapella</i> | 58 | 89 | 39 | 21.3509 |
| Sulphur-crested cockatoo | <i>Cacatua galerita</i> | 98 | 87 | 37 | 20.2646 |
| Little corella | <i>Cacatua sanguinea</i> | 14 | 93 | 43 | 19.5567 |
| Long-billed corella | <i>Cacatua tenuirostris</i> | 17 | 89 | 39 | 19.5098 |
| Pink cockatoo | <i>Cacatua leadbeateri</i> | 24 | 100 | 50 | 22.6742 |
| Yellow-tailed black cockatoo | <i>Calyptorhynchus funereus</i> | 7 | 100 | 50 | 23.6710 |
| Gang-gang cockatoo | <i>Callocephalon fimbriatum</i> | 38 | 100 | 50 | 30.9971 |
| Yellow rosella | <i>Platycercus f. flaveolus</i> | 6 | 100 | 50 | 30.6296 |
| Crimson rosella | <i>Platycercus elegans</i> | 17 | 23 | 27 | 31.5813 |
| Budgerigar | <i>Melopsittacus undulatus</i> | 9 | 51 | 1 | 59.7692 |
| Cockatiel | <i>Nymphicus hollandicus</i> | 20 | 90 | 40 | 28.0889 |
| Red-tailed black cockatoo | <i>Calyptorhynchus banksii</i> | 20 | 93 | 43 | 18.4779 |
| King parrot | <i>Alisterus scapularis</i> | 20 | 8.5 | 41.5 | 22.4216 |
| Palm cockatoo | <i>Probosciger aterrimus</i> | 5 | 80 | 30 | 26.3499 |
| Eclectus parrot | <i>Eclectus roratus</i> | 20 | 26 | 24 | 15.0394 |
| Turquoise parrot | <i>Neophema pulchella</i> | 10 | 45 | 5 | 33.4110 |
| Red-winged parrot | <i>Aprosmictus erythropterus</i> | 10 | 10 | 40 | 25.7329 |
| Australian ringneck | <i>Barnardius zonarius</i> | 5 | 20 | 30 | 28.6071 |
| Red-capped parrot | <i>Purpureicephalus spurius</i> | 5 | 72 | 22 | 31.4403 |
| Superb parrot | <i>Plytelis swainsonii</i> | 20 | 27.5 | 22.5 | 23.9352 |
| Red-rumped parrot | <i>Psephotus haematonotus</i> | 20 | 72 | 22 | 32.6547 |
| Little lorikeet | <i>Glossopsitta pusilla</i> | 15 | 49.3 | 0.7 | 39.6925 |
| Varied lorikeet | <i>Psitteuleles versicolor</i> | 5 | 48 | 2 | 38.6567 |
| Rainbow lorikeet | <i>Trichoglossus moluccanus</i> | 20 | 46 | 4 | 30.3341 |
| Bourke's parrot | <i>Neopsephotus bourkii</i> | 20 | 49.5 | 0.5 | 28.7778 |

The number of individuals scored varied considerably between species (see Table 1) due to differences in availability of birds to test. Both caged and wild birds were tested and, for all species apart from the budgerigar, data were collected from multiple locations in order to make the scores representative of the species.

The behavioural score was percent left-foot use to hold food. Brown and Magat [22] determined foot preferences by scoring the foot used to grasp food items, with 10 trials per individual bird. Rogers [21] scored the foot used to hold food while eating (Figure 2), the number of scores per individual varying from 1 to 6. Since budgerigars rarely hold food in a foot, in this species preferred foot was determined by placing a small piece of adhesive

tape on the dorsal surface of the beak and then scoring the foot used in attempts to remove the tape (10 scores per bird) [55].



Figure 2. Two left-footed cockatoos. **Left:** female red-tailed black cockatoo (*Calyptorhynchus banksia*). **Right:** male sulphur-crested cockatoo (*Cacatua galerita*). Note that the left foot grasps the food item and the entire leg is lifted to the beak (Photo credits: **left:** B. Machini, **right:** G. Kaplan).

The formula $(L/L + R) \times 100$ was used to determine % Left, where L refers to the number of times the left foot was used and R to the number of times the right foot was used. At least five subjects per species were assessed (Table 1). The scores determined were mean percentages for each species; hence, they represented the %L for each species, considered as a group or population.

Strength of foot preference was determined as the difference between the scored % Left and 50% (no preference). Hence, it was an absolute score, not taking into account the direction of the foot preference. These scores ranged from 0% to 50%.

Out of our main group of species, we selected for more detailed examination 11 species for which the volume of various brain regions, relative to the volume of the whole brain, had been determined using histological sections and Nissl staining by Iwaniuk and Hurd [56] (see Table 2). We selected to compare % Left and strength of foot preference with two brain regions: viz., the nidopallium (N) and the optic tectum. Data for these two regions were given as proportions of the total brain volume.

2.3. Statistical Tests

Pearson correlations (in Excel) were performed between % Left and brain mass relative to body mass ($\text{Brain mass/body mass} \times 1000$) and, in the smaller group, between % Left and the volumes of the two brain regions relative to total brain volume. Where needed, due to multiple comparisons, Bonferroni corrections were applied. Correlations were also made using scores for the strength of footedness (absolute value of difference between score and no preference, 50%).

Table 2. A list of the species in the sub-group tested for correlation between % Left foot use and the volumes of the nidopallium and the optic tecta relative to the volume of the whole brain (i.e., the scores are proportions). The figures for the two brain regions are given as proportions of the whole brain, sourced from Iwaniuk and Hurd [56].

| Common Name | Scientific Name | % Left | Nidopallium | Optic Tectum |
|------------------------------|---------------------------------|--------|-------------|--------------|
| Galah | <i>Eolophus roseicapella</i> | 89 | 0.3618 | 0.0314 |
| Yellow-tailed black cockatoo | <i>Calyptorhynchus funereus</i> | 100 | 0.3887 | 0.0196 |
| Cockatiel | <i>Nymphicus hollandicus</i> | 90 | 0.3571 | 0.0350 |
| Crimson rosella | <i>Platyercus elegans</i> | 23 | 0.3401 | 0.0429 |
| Budgerigar | <i>Melopsittacus undulatus</i> | 53 | 0.3210 | 0.0514 |
| Superb parrot | <i>Plytelis swainsonii</i> | 27.5 | 0.3200 | 0.0556 |
| Red-rumped parrot | <i>Psephotus haematonotus</i> | 72 | 0.3540 | 0.0387 |
| Rainbow lorikeet | <i>Trichoglossus haematodus</i> | 46 | 0.3370 | 0.0339 |
| Bourke's parrot | <i>Neopsephotus bourkii</i> | 49.5 | 0.3586 | 0.0482 |
| Australian king parrot | <i>Alisterus scapularis</i> | 8.5 | 0.3098 | 0.0424 |
| Eclectus parrot | <i>Eclectus roratus</i> | 26 | 0.3534 | 0.0351 |

3. Results

3.1. Association between Foot Preference and Body Mass

First, we tested our data to see whether they showed results similar to those of Brown and Magat [22] and, consistent with that report, strength of foot preference correlated significantly with body mass ($R(25) = 0.5339$, $p = 0.0059$, Bonferroni correction $\alpha = 0.0166$) and strongly with \log_{10} Body mass ($R(25) = 0.7166$, $p = 0.000056$). The larger the bird, the stronger the foot preference.

3.2. Association between Foot Preference and Brain Mass

Strength of foot preference correlated significantly with brain mass ($R(25) = 0.5259$, $p = 0.0069$, Bonferroni correction $\alpha = 0.0166$) and with \log_{10} Brain mass ($R(25) = 0.7166$, $p = 0.00005$; Figure 3A). Species with larger brains have stronger foot preferences. There was also a significant association between % Left and Brain mass ($R(25) = 0.4857$, $p = 0.01384$) and \log_{10} Brain mass ($R(25) = 0.4525$, $p = 0.02111$). Hence, left-footedness is stronger in species with a larger brain.

3.3. Association between Foot Preference and Brain Mass Relative to Body Mass

There was no significant correlation between % Left and brain mass/body mass ($R(25) = -0.1655$, $p = 0.4291$). However, the correlation between strength of foot preference and brain mass/body mass was significant ($R(25) = -0.6032$, $p = 0.0014$, Bonferroni correction $\alpha = 0.0166$; Figure 3B). The larger the size (or mass) of the brain relative to body size (or mass), the weaker the foot preference. This result comes about because body mass increases across species at a greater rate than does brain weight. Hence, species with larger bodies, and larger brains per se, but not relative to body mass, have stronger foot preferences.

3.4. Association between Foot Preference and Brain Mass in the Smaller Sample

First, this subset of 11 species was tested for Pearson correlation between the strength of foot preference and brain mass. As for the larger sample, this set showed a significant positive correlation ($R(11) = 0.6410$, $p = 0.0335$). This result shows that the subset was representative of the larger sample.

A Pearson correlation was applied to % Left scores versus relative volume of the nidopallial region and a positive association was found ($R(11) = 0.7674$, $p = 0.0058$, Bon-

ferroni corrected $\alpha = 0.025$; Figure 4A). Hence, the larger the volume of the nidopallium compared to the whole brain, the stronger the left foot preference.

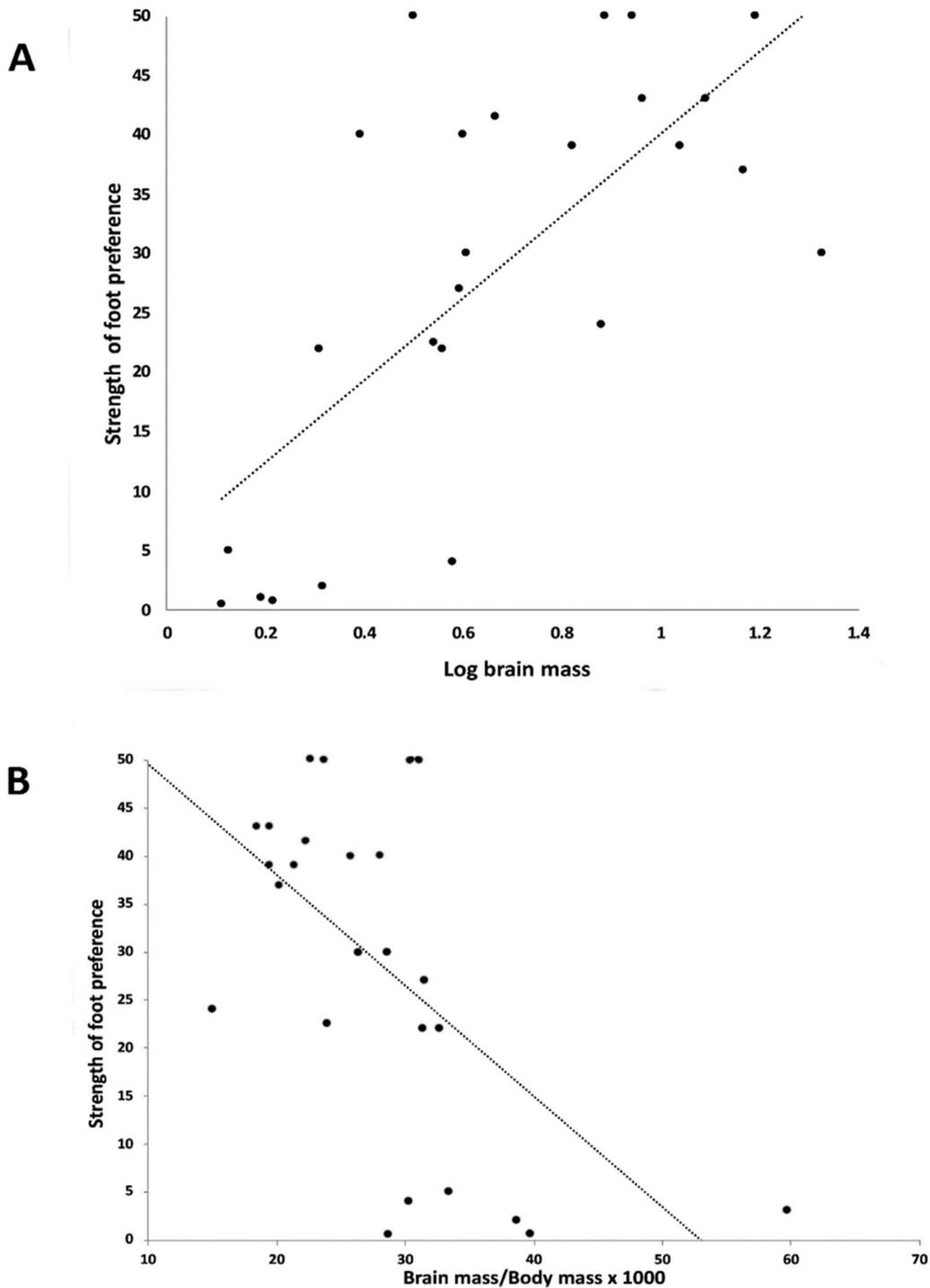


Figure 3. Strength of foot preference for the larger sample ($n = 25$) plotted against (A). Log_{10} of Brain mass, and (B). Brain mass/Body mass $\times 1000$. The correlation between Strength of foot preference and brain mass is significant and positive (see text) and between strength of foot preference and Brain mass/Body mass is negative and significant (see text).

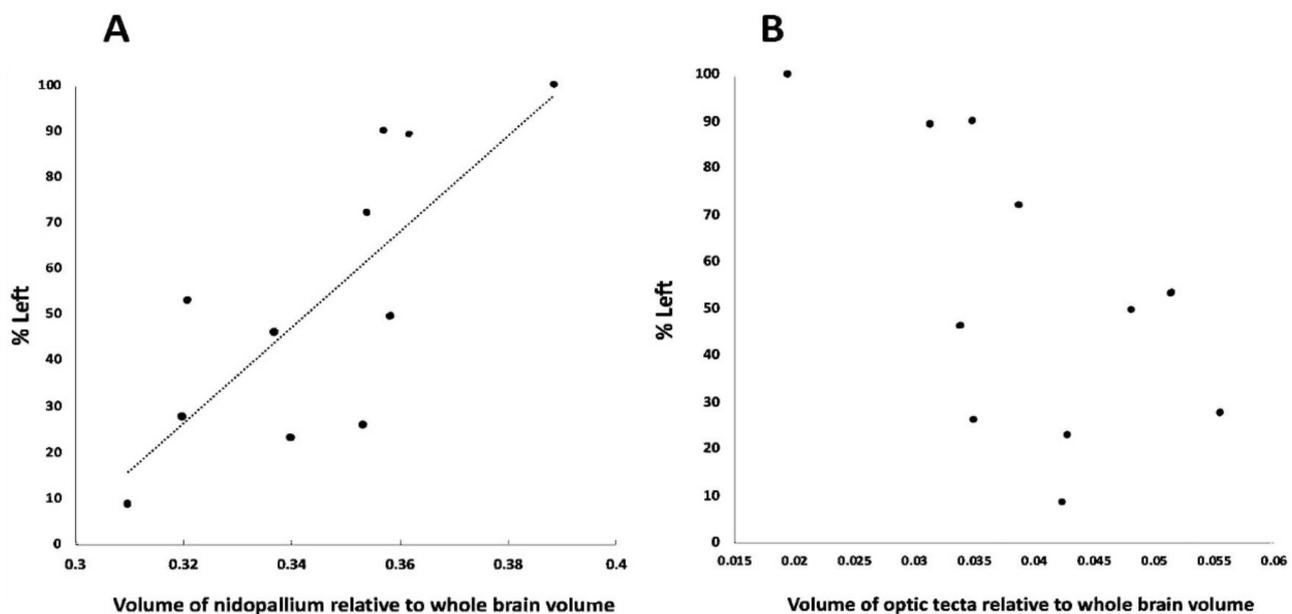


Figure 4. Percent left foot preference plotted against volume of the nidopallium relative to volume of the whole brain (A), and volume of the optic tecta relative to the volume of the whole brain (B). The positive correlation in A is significant: the nidopallium is larger, relative to the whole brain, in left footed parrots, and it is smaller in right-footed parrots. There is a trend for the opposite association between foot preference and size of the optic tecta but it is not significant after Bonferroni correction (see text).

A negative correlation was found between % Left and the relative volume of the optic tecta but it failed to be significant once the Bonferroni correction was applied ($R(11) = -0.6129$, $p = 0.0449$, Bonferroni correction $\alpha = 0.025$; Figure 4B).

Strength of foot preference did not correlate significantly with the volumes of either the nidopallium or optic tecta regions (nidopallium, $R(11) = 0.3393$, $p = 0.3072$; optic tecta, $R(8) = -0.5908$, $p = 0.0556$, Bonferroni correction $\alpha = 0.025$).

4. Discussion

First, we analysed the data to see whether they supported the finding of Brown and Margat [22] that, in species of Australian parrots, strength of foot preference correlates positively with body length, the latter being taken to indicate body size. As we were able to examine strength of foot preference versus body mass, this gave a better indication of the relationship between strength of foot preference and body size. By doing so, we found a significant positive correlation, which supports the findings of Magat and Brown [22]: the larger the species of parrot, the stronger is the foot preference. Magat and Brown [22] provided some evidence that this relationship may be due to larger parrots feeding on larger seeds. Such feeding would require more eye-foot manipulation. In fact, larger species often hold a whole seed pod in one foot and manipulate it carefully in order to extract the seeds (see Figure 1 in [57], p. 27, showing a yellow-tailed black cockatoo feeding on a large *Banksia* pod).

We also found a positive correlation between strength of foot preference and brain mass (Figure 3). The larger the brain size, the stronger the preference to hold food or objects in a preferred foot. In turn, this reflects control by the hemisphere opposite the preferred foot and use of the specific specialised functions of that hemisphere. However, the association between strength of foot-preference and brain mass relative to body mass is negative (Figure 3). To summarise the results so far, although larger birds have stronger foot preferences and larger brains, they have smaller brain mass relative to body mass: this means that, across species, the body size increases at a greater rate than does brain size.

These measures may also correlate with other factors; for example, with genome size and, hence, neuronal complexity of the brain. In fact, Andrews and Gregory [58] found that, in 54 species of parrots and cockatoos, genome size correlated negatively with relative brain size. They attributed this to species differences in neuronal complexity: the larger the genome, the more complex are the neural connections in the brain [58]. It would now be worth investigating whether a similar association between brain size and genome size holds for the species we tested. Since we have found a negative correlation between strength of footedness and relative brain mass, strength of foot preference may correlate positively with genome size, and hence, complexity of brain structure. This is merely a thought for future research. We are aware that whole brain size is a rough measure to associate with behaviour [59] but it is a starting point leading to investigation of more specific brain regions associated with particular patterns of behaviour.

Our findings also illustrate the difference between using absolute brain size compared to relative brain size when drawing links between brain and behaviour [60]. We suggest that absolute brain size (or mass) is a better measure to associate with foot preference, and possibly also with cognitive behaviour, than is brain mass relative to body mass. As Herculano-Houzel [61] emphasised, body mass is very variable and not tightly correlated with the number of neurones in the brain. Nevertheless, although it is preferable not to use body mass as a measure related to behaviour or cognition, within Psittaciformes, Herculano-Houzel [61] did report a positive relationship between the number of neurones in the brain and body mass and, more specifically, between the number of neurones in the pallium and body mass. To extrapolate to our data, since foot preferences are stronger in larger parrots with larger brains, these features may go along with more neurones in the brain and with higher computational capacity or “cognitive power” [36].

The positive relationship between strength of foot preference and brain mass was also present in our subgroup of 11 species selected in order to examine correlations between foot preference and regional areas of the brain. In this representative subgroup, we also found that % Left correlated positively with volume of the nidopallium relative to whole brain volume (Figure 4). Parrots with proportionately larger nidopallial regions express stronger left-foot preferences, and hence use of the right hemisphere. Put simply, the nidopallium is larger in left-footed species than it is in right-footed species.

The nidopallial region measured by Iwaniuk and Hurd [56] included all of the subregions (nucleus basorostralis pallii, entopallium and arcopallium) as well as area temporo-parieto-occipitalis. The entopallium is a primary visual centre, receiving inputs from the retina, via the optic tectum and nucleus rotundus, and sending outputs to the arcopallium (see Figure 1), which in turn sends outputs to the brain stem and controls motor function (summarised in [28]). It is a visuo-motor system clearly involved in eye-foot co-ordination. It is not known whether these regions of the nidopallial complex differ in size between the hemispheres, and so may be associated with asymmetry of limb use, but research on pigeons has shown that asymmetry is present in the visual pathway sending inputs to the entopallium: the entopallium in the left hemisphere receives strong inputs from both eyes, whereas the same region in the right hemisphere receives inputs mainly from the left eye [28,62,63]. In left-footed birds, therefore, the right hemisphere is being used rather exclusively to carry out eye-foot co-ordination needed to hold and manipulate food items [52].

Recently, Morandi-Raikova et al. [64] reported asymmetry in entopallial neurones in domestic chicks: they found more parvalbumin-expressing neurones, most likely GABAergic inhibitory neurones, in the entopallium of right hemisphere than in the same region of the left hemisphere. This suggests that primary visual inputs are processed differently in the left and right hemispheres. Furthermore, as shown in the pigeon, there is asymmetry in the arcopallial regions, due to differences in left-to-right versus right-to-left exchange of visual information via the anterior commissure [65].

We found a trend for a negative correlation between % Left and the relative size of the optic tecta (Figure 4) but it was not significant in our sample, perhaps due to our small

sample size. Nevertheless, the larger nidopallium, as we found in species with stronger foot preferences, is not matched by any difference between species in size of the optic tecta. It seems, therefore, that visual processing in the optic tecta may well be similar across species. Hence, there is regional specificity in size increase of the nidopallium related to foot preference. Our data provide an example, across species, of brain structures contributing differently to whole brain size, a consideration discussed in detail by Willemet [60].

It is not known whether evolution of the bird brain involved coordination between the telencephalon and non-telencephalic regions [54] but this seems highly unlikely. The latter is not necessarily related to cognition. From Striedter and Charvet's work [66], we have evidence that certain areas of the brain differ in size relative to the rest of the bird's brain in different species from embryonic stage onwards. In a morphometric comparison between budgerigars, *Melopsittacus undulatus*, and quails, *Colinus virginianus*, the researchers showed [66] that species differences in telencephalon and optic tectum size occur right from the beginning of development of the embryo: the optic tectum being much larger in the quail than in the budgerigar, whereas the telencephalon occupies more than 60% of the budgerigar brain and slightly more than 40% in the quail [66]. These differences reflect the cognitive differences between budgerigars and quails.

The evidence is already clear that parrots have brain/body ratios and encephalization quotients similar to those of primates [54]. However, in most research on the size of the telencephalon and sub-structures, there has been no consideration of differences between the left and the right hemispheres. Apart from a recent study of cichlid fish, showing associations between lateralized behaviour and brain structures, as well as gene expression [67], research on asymmetry in non-human species has focused on left-right differences in function rather than structure.

In a range of species, the left hemisphere has been shown to be responsible for top-down control (such as routine behaviour) and the right hemisphere for environmentally elicited behaviour such as response to threats and social partners [68]. Social play behaviour in parrots and other clades is correlated positively with brain size [69] but, for this behaviour, there has been no study of differences between the hemispheres. By contrast, social recognition is known to be largely right-hemisphere controlled [70,71] and, as Yamazaki et al. [72] concluded, cognition overall may be largely asymmetrical [73].

The significant results shown here concern the relationship between footedness and the size of the nidopallium, a region of the forebrain with executive and other higher-level functions. Our finding, coupled with the evidence of parrots' exceptional vocal and cognitive abilities, indicates that the nidopallium deserves more and detailed attention. Our finding of a significant positive correlation between % Left foot use and the size of the nidopallium further suggests that it would be worth looking in future for asymmetries in the size of the nidopallial regions of the hemispheres and, particularly, the areas that are included in that region, the entopallium, arcopallium and NCL. We hope that our findings might encourage future research on left-right differences, not only of gross structure, but also of neural processing [74], subcellular structures [64] and gene expression [67].

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